

ANNALS OF THE UNIVERSITY OF STELLENBOSCH

Edited by
PROF. C. A. DU TOIT

Co-editors:
**PROF. J. F. KIRSTEN, PROF. J. A. J. VAN RENSBURG
and PROF. R. W. WILCOCKS**

Volume 29, Section A, No. 4 (1953)

ONTOGENESIS and MORPHOGENESIS OF THE BREAST-SHOULDER APPARATUS OF XENOPUS LAEVIS

by
R. VAN PLETZEN

Zoological Institute, University of Stellenbosch, South Africa.

Price 7/-

**ANNALS OF THE UNIVERSITY
OF STELLENBOSCH**

Volume 29, Section A, No. 4 (1953)

**ONTOGENESIS and MORPHOGENESIS
OF THE BREAST-SHOULDER APPARATUS**

OF

XENOPUS LAEVIS

by

R. VAN PLETZEN, D.Sc.

Zoological Institute, University of Stellenbosch, South Africa

With 23 text-figures

Submitted: June, 1950

Abstract

The chief results of this investigation are concerned with the problem of sternogenesis which has continually been the object of research since the time of Georg Ruge. For the first time the importance of the ventral fascia of appendicular hypaxonic musculature for the non-zonal elements of the breast-shoulder apparatus receives due consideration. Fundamental problems of the origin of the sclerogenic components of the limb-bud are fully discussed. The purely descriptive anatomy of the breast-shoulder apparatus of *Xenopus*, in view of the interest attaching to its ossa investitientia, has also been investigated. The recent paper of Jui Ming Chen on mammalian sternogenesis arrived too late for consideration. (Journal of Anatomy, vol. 86, pt. 4 and vol. 87, pt. 2.) It confirms the results obtained for *Xenopus*, for it also rejects the Ruge hypothesis of the costal origin of the sternum.

CONTENTS

	Page
1 Introduction	139
2 Historical review	144
3 Material and technique	145
4 The anatomy of the adult breast-shoulder apparatus	147
5 The development of the shoulder-girdle	155
Stage A	155
Stage B	158
Stage C	158
Stage D	160
Stage E	161
Stage F	162
Stage G	163
6 The development of the sternum	168
Stage A	168
Stage B	169
Stage C	170
Stage D	171
Stage E	172
7 Summary and conclusions	175
8 Alphabetical list of abbreviations	179
9 List of literature cited	180

INTRODUCTION

The term "breast-shoulder apparatus" was coined by Fürbringer (1876) to denote the shoulder-girdle plus the sternum and episternum. It does not follow, however, that Fürbringer meant these structures to be morphogenetically related.

In reviewing the literature dealing with the anuran breast-shoulder apparatus, I do not intend to give a detailed account of the older literature, as it has been very fully dealt with by De Villiers (1922, 1925). The reader is referred to these works for a comprehensive review of the work of the older anatomists and embryologists. The nomenclature used in this work is that employed by De Villiers (1922).

It is now the general practice to divide the anuran shoulder-girdle into a dorsally situated pars scapularis and a ventrally situated pars coracoidea. The pars scapularis comprises the os scapulare and the cartilago suprascapularis, the latter partly covered on its outer, and to some extent on its inner, aspect by an os investitiens, the cleithrum. The pars coracoidea consists of an anterior bar, the cartilaginous or sometimes ossified procoracoid with its os investitiens, the clavícula, and the posterior bar or coracoid, which in anurans is always ossified. The medio-ventral ends of the procoracoid and of the coracoid are connected with each other by means of the cartilaginous processus epicoracoideus, thus enclosing a fenestra obturatoria in the pars coracoidea of the shoulder-girdle. According to Götte (1877) and Fuchs (1927) the processus epicoracoideus is to be regarded as a forwardly directed process of the os coracoideum or actually its unossified homologue.

Gegenbaur (1865) was not aware that the so-called "perichondral ossification of the suprascapula" is a membrane bone, but he knew that the procoracoid and the clavícula are separate entities, separated from each other by means of a thin layer of connective tissue. That the cleithrum and clavícula are in reality ossa investientia was first realised by Braus (1909, 1919) and was fully confirmed by Schmalhausen (1917), De Villiers (1922) and Fuchs (1922). The discovery of the true nature of the cleithrum is of great phylogenetic importance, as it brings living *Amphibia* into line with the *Labyrinthodontia*, in which such a bone was always present. In all his works on the anuran breast-shoulder apparatus Fuchs calls the clavícula the os thoracale. This change of nomenclature is based on his important discovery (1912) that the clavícula of the *Mammalia ditremata* is not a pure os investitiens, as is the case in most *Anura*, but that it is a bone of composite origin, since pieces of cartilage, which are regarded as vestiges of the cartilago procoracoidea, are incorporated in the developing clavícula. The term "clavícula" used in human anatomy can only be used for such osseous elements in lower vertebrates in which a structure histogenetically homologous with the human clavicle occurs. This is actually the case in some *Anura* (Fuchs, 1922), in which the separating connective tissue between the anuran clavicle and the procoracoid disappears, so that there is an invasion of the

cartilage by the os investitiens. The cartilage subsequently ossifies and fuses with the anuran clavicle, thus forming a bone of mixed origin, much as in the human clavicle (B.N.A.). Fuchs (1922) claims that ossification of the procoracoid proceeds from the clavicle after the separating connective tissue has been broken through, but De Villiers (1929) was able to demonstrate that the cartilago procoracoidea in *Xenopus* can undergo independent ossification, the separating membrane between clavicle and underlying cartilago procoracoidea remaining intact.

The fenestra obturatoria, situated in the pars coracoidea of the shoulder-girdle and enclosed by the coracoid, procoracoid and processus epicoracoideus is supposed to arise in at least two different ways in *Anura*. According to Götte (1877) and Fuchs (1927) the coracoid and procoracoid in *Rana* arise ontogenetically from the glenoid part of the pars scapularis as two separate, ventrally directed processes. The ventral end of the cartilaginous coracoid subsequently flattens out in the direction of the cartilago procoracoidea, thus forming the processus epicoracoideus. The latter then fuses with the medio-ventral end of the cartilago procoracoidea to form a fenestra obturatoria medio-ventrally. This fenestra is then regarded as a primary fenestra ("Sprossungsfenster" of Fuchs), covered in some *Anura* at least by a membrana obturatoria, which originates from the surrounding connective tissue not belonging to the shoulder-girdle and therefore regarded as a secondary membrane ("Fibrogene Membran" of Fuchs). Secondary fenestrae ("Reduktionsfenster" of Fuchs) in the pars coracoidea of the shoulder-girdle are said to be present in lizards, and are covered by primary membranes (Fuchs, 1927). Ontogenetically these secondary fenestrae are regarded by Fuchs as unchondrified parts of a broad, flat pars coracoidea. The unchondrified connective tissue filling up these secondary fenestrae gives origin to the membranes covering the latter in the adult. Such membranes originating from connective tissue belonging to the shoulder-girdle itself are known as primary membranes ("Reduktionsmembranen" of Fuchs). As stated above, Fuchs regards the fenestra in the lacertilian shoulder-girdle as secondary, and maintains that these reptiles therefore lack a procoracoid and a processus epicoracoideus. He further regards the anuran and chelonian fenestra and procoracoid as being homologous structures, while Goodrich (1930) maintains that the chelonian procoracoid is a very long processus acromialis. I do not intend to discuss this old controversy in comparative anatomy: the exact homologues of the different parts of the reptilian shoulder-girdle. For further details the reader is referred to the works of Van Gelderen (1923, 1925). It should also be mentioned that Anthony and Vallois (1914) deny the homology of the coracoid and procoracoid in urodeles and anurans, but later workers on the urodelan shoulder-girdle, such as Engler (1929) and Hoffman (1936) see in the urodelan coracoid and procoracoid the exact homologues of these structures in anurans.

According to Braus (1909) and Nauck (1928) the fenestra obturatoria in *Bombina(tor)* and *Alytes* arise in quite a different manner from that described by Fuchs and Götte for *Rana*. The fenestra in these two genera arises very early during ontogeny, when the whole pars coracoidea of the shoulder-girdle is still in a blastematous or procartilaginous condition. At this stage the pars coracoidea is pierced by a foramen for the transit of the nervus supracoracoideus and of blood-vessels supplying the hypaxonic

appendicular muscles situated on the outer aspect of the shoulder-girdle. The coracoid, procoracoid and processus epicoracoideus subsequently chondrify round the foramen, which enlarges during ontogeny, and eventually forms the fenestra obturatoria in the adult.

The relationship of the two processûs epicoracoidei to each other ventrally is of great importance. Cope (1865) and Boulenger (1882) used it as a basis of classification, and although their systems are now antiquated, the terms "*Firmisternia*" and "*Arcifera*", first instituted by Cope, are still in use today to denote the two main phylogenetic trends along which the shoulder-girdle of modern anurans has developed. The *Arcifera* are those anurans in which the two processûs epicoracoidei overlap and are movably articulated to each other in the mid-ventral line, while the *Firmisternia* are those in which the processûs epicoracoidei are either fused or firmly cemented to each other in the mid-ventral line. Fuchs (1926 b) and Howell (1935) state that the proto-amphibian condition was undoubtedly the firmisternal type, while Noble (1922) and De Villiers (1924, 1929) maintain that the arciferous type of epicoracoidal articulation is the primitive condition. If the latter is actually primitive, the firmisternal type is to be considered as derived from the arciferous type, and it is also to be expected that at least some firmisternal anurans should recapitulate an arciferous stage during ontogeny. This is exactly what happens during the development of *Kaloula* and *Rana*, two diplasiocoelous genera (Hsiao, 1933-1934). Noble (1926) observed the same phenomenon in some brachycephalid frogs. De Villiers (1924, 1929) failed to observe any overlapping of the processûs epicoracoidei in developmental series of *Breviceps* and *Rana*, and assigns no great phylogenetic value to arcifery. The aglossal opisthocoelous genera *Xenopus* and *Pipa* seem to occupy an intermediate position between the arciferous and firmisternal types as they are arcifero-firmisternal, while *Hymenochirus* is typically firmisternal (De Villiers, 1929). Noble (1926) finds that arcifero-firmisterny also characterises the *Brachycephalidae* and the Chinese ranid, *Rana rugulosa*.

As stated above, the classifications of Cope (1865) and Boulenger (1882) are now antiquated. Noble (1922) proposed a more natural classification based on the structure of the vertebral column and the thigh musculature. This system is now generally accepted, and Hsiao (1933-1934) has pointed out that the comparative study of the musculature and osteology of the pectoral region in the Chinese *Salientia* results in the same "phylogenetic tree" as the one of Noble (1922) based upon the pelvic region.

Of great importance is the ontogeny of the fibrous connective tissue situated interepicoracoidally and binding the processûs epicoracoidei and the sternum together. According to Fuchs (1926 b) this tissue originally stretched from the posterior edge of the episternum to the anterior edge of the sternum, and probably represents a vestige of a skeletal piece originally intercalated between the two ventral halves of the girdle. He considers this tissue and the sternum as originally costal in origin, although his view is not supported by more recent ontogenetic studies. De Villiers (1929) maintains that the binding tissue is the mother tissue of the sternum in *Xenopus*, and is a derivative of the linea alba. Roggenbau (1926) describes an extensively vascularised type of intercoracoidal binding tissue in *Rana*, and believes that it represents a vestige of an interclavicle, an unpaired dermal bone present in the ventral part of the shoulder-girdle of

Labyrinthodontia, of extinct and of some modern *Reptilia*, and even of *Monotremes* (Romer, 1931, Broom, 1932). He bases his conclusion on the histological structure of the tissue. De Villiers (1929) finds a similar kind of tissue in *Xenopus*, but it is situated interprocoracoidally. He denies its affinity to the interclavicle and maintains that connective tissue subjected to stress and strain may undergo histological differentiation approximating to that which is passed through by tissue destined to give rise to bone by direct ossification (os investitiens).

The ontogeny of the vertebrate sternum and episternum remains one of the most disputed points in comparative anatomy. The classical theory of the origin of the sternum is Ruge's costal theory (1880), confirmed by Knopfli (1919) for birds and Juhn (1923) for lizards. This theory, however, has been discredited by a large number of workers, such as Bogoljubski (1914), Whitehead and Waddell (1911), Hommes (1921), Van Gelderen (1925) and Kälin (1929). The latest investigations on the reptilian sternum are those of the last two workers. Van Gelderen (1925) regards the anterior part of the reptilian and the amphibian sternum as being autochthonous, and the posterior part of the reptilian sternum (xiphisternum) as being of costal origin. In direct contrast to his views are those of Kälin (op. cit.) who derives the crocodilian sternum entirely from the coracoids. Götte (1877) postulates a zonal origin for the anuran sternum, Wiedersheim (1892) and Lignitz (1897) derive the sternum from myocommatous tissue, while Parker (1891) stated that it is partly of zonal and partly of myocommatous origin. De Villiers (1922), the first worker of the Zürich school to break away from Ruge's costal theory, was able to show that the sterna of *Bombina*(*tor*) and *Alytes* are partly of zonal and partly of myocommatous origin, and suspected that the sterna of *Xenopus* and *Hyla* have a similar origin, while that of *Rana* was to be regarded as an unpaired chondrification of the linea alba. Engler (op. cit.) still advocates a costal origin for the sternum in urodeles, although he shows that the sterna of *Salamandra atra*, *Salamandra maculosa* and *Molge alpestris* are autochthonous chondrifications of the linea alba. Hoffmann (op. cit.) denies the costal and even the linea alba origin of the sternum in urodeles, and states that it is partly of zonal and partly of myocommatous origin. Recently Gladstone and Wakeley (1932) totally discarded the costal theory and state that in all *Vertebrata* the sternum arises as two mesodermal plates or sternal bars, situated in the lateral part of the body wall. These bars later fuse in a cranio-caudal direction to give rise to the unpaired condition in the adult.

The episternum, phylogenetically regarded as the most recent structure in the anuran breast-shoulder apparatus, is usually better developed in the *Firmisternia* than in the *Arcifera*. W. K. Parker (1868), Götte (1877), T. J. Parker (1891) and Fuchs (1926 b) regard the episternum as being of zonal origin, whereas Wiedersheim (1892), Lignitz (1897), De Villiers (1922), Gladstone and Wakeley (1932) and Hoffman (1935) believe that the episternum arises as a chondrification of the linea alba anterior to the shoulder-girdle.

It would therefore seem that the sternum and episternum of *Amphibia* can originate in different ways, and that skeletal elements lying in the linea alba in the same topographical position, are not necessarily to be regarded as derivatives of the linea alba. This view is further supported by the development of the epipubis of *Xenopus*, *Liopelma* and *Ascaphus*, the ypsiloid apparatus

of some urodeles, and the processus epipubicus of *Necturus*. The epipubis of *Xenopus* and the ypsiloid apparatus arise as paired chondrifications of the linea alba anterior to the pelvic girdle (De Villiers, 1925), while the processus epipubicus of *Necturus*, occupying the same topographical position as the epipubis and ypsiloid apparatus, is of zonal origin (Hoffman, 1935). De Vos (1938) maintains that the epipubis of *Liopelma* may also be of a linea alba origin.

The ontogeny of the tissue forming the earliest anlage of the limb-bud is still a vexed problem. It is well-known that the vertebrate skeleton, apart from chitinous or calcareous derivatives of the ectoderm and the enamel of the teeth, is of mesodermal origin, and that the zonal and appendicular skeletons develop from one and the same anlage. De Villiers (1926) maintains that it is almost a certainty that the limb-bud tissue in *Xenopus* is of mesenchymatous origin, as in the connective tissue phase the girdle anlage, the vertebral column and the myocommata are in direct continuity with one another. Braus (1904) also believes in a mesenchymatous origin of the limb-bud tissue, and states that in all *Vertebrata* the anlage of the shoulder-girdle arises as a blastematous cell-thickening in the mesenchyme of the body wall. Goodrich (op. cit.) states that in fishes, *Amphibia* and in many of the higher *Amniota* the girdle and limb-musculature arise as cell proliferations from the ventral ends of the myotomes, such proliferations combining to form a continuous mass and later giving rise to two plates from which the muscles of the girdle and fore-limb develop.

The chief questions pertaining to the breast-shoulder apparatus of *Xenopus* to be discussed below are the following:

- 1 The origin of the tissue forming the earliest anlage of the limb-bud.
- 2 The relation of the clavícula to the cartilago procoracoidea, and the presence or absence of ossification in the latter.
- 3 The ontogeny of the fenestra obturatoria and of the processus epicoracoideus.
- 4 The origin of the fibrous connective tissue binding the ventral halves of the girdle to each other.
- 5 The ontogeny of the sternum.

HISTORICAL REVIEW OF THE INVESTIGATIONS ON THE BREAST-SHOULDER APPARATUS OF *XENOPUS LAEVIS*

A detailed discussion of the work on the breast-shoulder apparatus of *Xenopus* by older anatomists such as Stannius (1865), W. K. Parker (1868), Mivart (1869), Fürbringer (1873-1874) and Boulenger was given by De Villiers (1924). It should be remembered that all these workers, except possibly Boulenger, regarded the shoulder-girdle of *Xenopus* as being firmisternal, and Parker (op. cit.) observed a discontinuity in the processûs epicoracoidei, a condition which was later confirmed by Fürbringer (op. cit.).

Proctor (1921) studied the scapula in the *Aglossa*, and concluded that that of *Xenopus* is vestigial or apparently occasionally absent, a condition that she explains as having arisen through the fusion of the scapula with the "praecoracoid" (clavicula?).

De Villiers (1922, 1924, 1925, 1929) devoted much attention to the anatomy and development of the *Xenopus* breast-shoulder apparatus. In 1922 he partly investigated the anatomy of the breast-shoulder apparatus and the development of the sternum, and concluded that the girdle is arcifero-firmisternal; as to the origin of the sternum he suggested that since in *Bombina(tor)* the sternum arises as four cartilaginous nodules (two of them being of zonal and two of myocommatous origin) the sternum of *Xenopus* might originate in a similar manner.

In 1924 the same author reinvestigated the anatomy of the adult breast-shoulder apparatus, and maintained that the ventral halves of the shoulder-girdle are definitely articulated on the arcifero-firmisternal principle, that arcifery is probably a primitive feature, and that the procoracoidal cartilages sometimes show insipient ossificatory processes. A discontinuity of the processûs epicoracoidei was not observed, although a large number of specimens were microtomed or dissected.

In 1925 De Villiers studied the development of the epibus, discussed the possible origin of the connective tissue constituting the linea alba, inscriptiones tendineae and myocommata, and concluded that the connective tissue of these entities probably originated from the sclerotome. He also stated that both the epipubis and the sternum are paired chondrifications of the linea alba. The same author's investigations of 1926 revealed that the anlagen of the limb-bud and of the girdle are in syndesmotic continuity with the myocommata and the anlage of the vertebral column, a fact which probably indicates that the limb-bud and the girdle tissues are of mesenchymatous origin.

Certain aspects of the shoulder-girdle was reinvestigated by De Villiers (1929), in the light of Fuch's statement (1926 b) that ossification of the procoracoid cartilage proceeds only after the limiting membrane between it and the clavicula has broken down. The investigation revealed that in *Xenopus* at least, the procoracoidal cartilages definitely ossify although the limiting membrane remains intact. It was also found that the interprocoracoidal tissue may be a linea alba derivative, that it is sometimes extensively

canaliculised, and that the canaliculi do not contain blood. The shoulder-girdle of *Pipa* as well as that of *Hymenochirus* was also investigated and compared with that of *Xenopus*, and it was concluded that the shoulder-girdles of these three representatives of the Pipidae constitute a series, characterized by the progressive fusion of the processûs epicoracoidei. This fusion probably results in the progressive immobility of these cartilages, and probably eventually leads to firmisterny, which has already been attained by *Hymenochirus*.

De Villiers does not claim that the series mentioned above is a phylogenetic one, since the present dispersal of these three aglossal genera does not support such an assumption: *Xenopus* and *Hymenochirus* being aethiopian genera, while *Pipa* is neotropical.

In addition to the works mentioned above, the following investigations were carried out in connection with *Xenopus*: Dreyer (1914) studied the morphology of the tadpole, Grobbelaar (1924) investigated in detail the entire musculature of *Xenopus*, Noble (1922, 1925, 1926 (a), 1931) gave a general description and an account of the systematic position and probable phylogeny of the *Aglossa*, Van der Horst (1931) reported on the lateral-line nerves of *Xenopus*, Kotthaus (1933) and Paterson (1939) studied the development of the chondrocranium, while Millard (1941, 1949) investigated in detail the vascular anatomy and development of the venous system of *Xenopus*. In addition to investigating the development of the chondrocranium, Paterson (1939, 1941) also paid attention to the olfactory organ, tentacles and anterior blood-vessels of *Xenopus*. The essential neotenic origin and organisation of the *Aglossa*, profoundly influencing all anatomical and ontogenetic work on the group, was expressed most clearly by Escher (1925).

MATERIAL AND TECHNIQUE

It is a well-known fact that the size of anuran larvae is not a true criterion of the degree of development attained by the different systems of organs. Measurement of the larvae is therefore of little consequence in determining the age of developmental stages, although this is the usual method employed in descriptive embryology. De Villiers (1922) employed the degree of development of the legs and the length of the tail in determining the different developmental stages of *Bombina(tor)*. I have also adopted this method for *Xenopus*, but in addition each larva was measured. In older postmetamorphic specimens in which the tail has been resorbed entirely, the measurement was made from snout to cloacal aperture. The diagrams on the following two pages represent the different stages into which the material has been classified.

The material was collected in the vicinity of Stellenbosch, fixed in 8% formol and preserved in 4% formol. It should be mentioned that it was never found necessary to remove the alimentary canal before sectioning, even in larvae with a very large, spirally coiled intestine.

Decalcification of the material is always necessary, even in the youngest larvae, as the sacci endolymphatici, containing calcium carbonate crystals, arise early in ontogeny. For decalcification Ebner's fluid or an alcoholic solution of nitric acid (5% — 10%) was used, the latter being preferable, as nitric acid decalcifies more quickly than Ebner's fluid, and

DIAGRAM 1: DEVELOPMENT OF THE SHOULDER-GIRDLE

Stage	Length		Short description.
	(a)	(b)	
	From snout to tip of tail.		
	From snout to cloacal aperture.		
A	(a) 8 mm. (b) 18.4 mm.		Pectoral and Pelvic limb-buds both indistinguishable.
B	(a) 12.5 mm. (b) 31.6 mm.		Pectoral limb-buds indistinguishable. Pelvic limb-buds distinguishable and enclosed in atrial cavities.
C	(a) 15.9 mm. (b) 40.3 mm.		Pectoral limb-buds distinguishable. The latter and pelvic limb-buds enclosed in atrial cavities.
D	(a) 19.2 mm. (b) 44.2 mm.		Front legs distinguishable, enclosed in atrial cavities. Hind legs free, but not in use.
E	(a) 20.1 mm. (b) 48.2 mm.		Front legs still enclosed in atrial cavities, hind legs larger than in stage D, but not yet in use.
F	(a) 25.7 mm. (b) 60.6 mm.		Front legs free but not in use. Hind legs large and in use. Tail and intestine have attained maximum state of development. Head very broad and flat.
G	(a) 21 mm. (b) 59 mm.		Front and hind legs both well developed and in use. Intestine less spirally coiled and metamorphosis moderately far advanced.

DIAGRAM 2: DEVELOPMENT OF THE STERNUM

Stage	Length		Short description.
	(a)	(b)	
	From snout to tip of tail.		
	From snout to cloacal aperture.		
A			Corresponds to stage F in diagram 1.
B			Corresponds to stage G in diagram 1.
C	(a) 19.1 mm. (b) 32 mm.		Front and hind legs well developed and in use. Tail in process of reduction. Metamorphosis far advanced. Spirally coiled intestine reduced.
D	(a) 19 mm. (b) 25.6 mm.		Tail shorter than in previous stage, metamorphosis further advanced than in previous stage.
E	(a) 16.5 mm. (b) Id.		Tail entirely resorbed. Metamorphosis completed.

as aqueous decalcifiers were found to be less satisfactory. For larger post-metamorphic specimens the nitric acid concentration may be increased up to 12% to obtain complete decalcification in a relatively short time without deleterious effects. Methyl-benzoate-celloidin or cedar-wood oil was used as a clearing agent. Paraffin with a m.p. of 48°C is most suitable for embedding larvae and small postmetamorphic specimens, but for larger specimens a paraffin of a m.p. of at least 52°C should be employed.

It is a notorious fact that *Xenopus* material is difficult to stain, this probably being the result of the neotenic nature of the tissues; this is especially true if azan is used. The latter is a very useful stain for studying morphological details in postmetamorphic material and for ossification processes, such as the development of membrane bones, as the aniline blue stains even the smallest anlage of bone intensely blue. This stain gives the best results when used in combination with borax-carmin. Staining with azan, however, is rather a laborious process, as it requires a mordant, preferably phosphotungstic acid, and as the latter is used in an aqueous solution, dehydration with alcohol is imperative. Instead of the azan combination the haemalum-Bismarck-brown combination may be used especially for larval stages, in which processes of chondrification are to be studied. For adult specimens the latter two stains may also be used in combination with other plasmal stains, such as light-green and/or eosin. As these stains are all soluble in 95% alcohol laborious dehydration is largely obviated.

The sections were cut 10 μ , 12 μ and 15 μ in transverse, frontal and saggital series, and reconstruction drawings were made by means of an apparatus copied by Prof. C. A. du Toit from that used by Pusey.

The investigation has been carried out under the supervision of Prof. Dr. C. G. S. de Villiers. I wish to thank him most sincerely for his assistance and valuable advice. My sincere thanks are also due to Prof. T. F. Dreyer and Dr. M. E. Malan for reading the script.

THE ANATOMY OF THE ADULT BREAST-SHOULDER APPARATUS

The most recent descriptions of the anatomy of the adult breast-shoulder apparatus following those of Stannius (1856) and Parker (1868), are those of De Villiers (1924, 1929), and the reader is referred to these works for a detailed account. Certain important points, however, deserve further discussion.

Nothing new is to be reported on the supracapula, cleithrum and coracoid, except that in the shoulder-girdle of very large specimens the connective tissue between the supracapula and the cleithrum partly disappears, resulting in the invasion of the cartilage by the investing membrane bone, and the subsequent ossification of the former (see fig. 3). This condition obtains in that part of the supracapula in which the cartilaginous joint with the dorsal tip of the scapula is located. The hinge, however, is not entirely affected by the ossification: a strip of cartilage between scapula and supracapula remains cartilaginous (Fig. 3, cj). The large, characteristically V-shaped cleithrum in the *Aglossa* is quite remarkable, as it is in most *Anura* a narrow flange of membrane bone, covering the outer aspect of the supracapula. This feature may perhaps be considered as primitive, as a large cleithrum is typically present

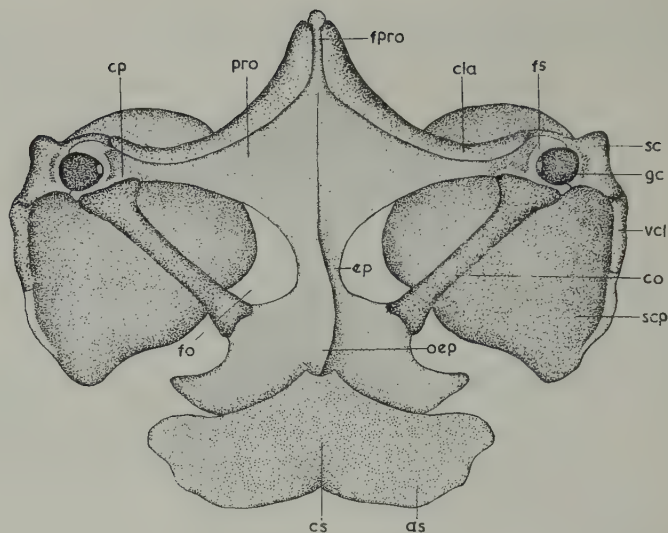


FIG. 1

Graphic reconstruction of the breast-shoulder apparatus of an old postmetamorphic specimen, ventral aspect. X 13. as: lateral wing of the sternum; cla: clavícula; co: coracoid; cp: cartilago paraglenoidalis; cs: corpus sterni; ep: processus epicoracoideus; fo: fenestra obturatoria; fpro: fused parts of the procoracoid cartilages; fs: glenoid foramen; gc: glenoid cavity; oep: overlapping parts of the processus epicoracoidei; pro: procoracoid cartilage; sc: scapula; scp: suprascapula; vcl: ventral flange of the cleithrum.

in many extinct and modern fishes and in *Labyrinthodontia* (Romer, 1931, Jarvik, 1944). However, in the *Liopelmidae*, which are regarded as more primitive than the *Aglossa*, the cleithrum is relatively much smaller than in the *Aglossa* (De Vos, op. cit.). Is it possible that the large cleithrum of the *Aglossa* is correlated with a small scapula, while the small scapula is in turn correlated with the aquatic habit of existence, which is certainly a neotenic feature? In any case, the cleithrum still has an important function, serving to a large extent as the point of attachment for a large number of muscles associated with the shoulder-girdle and with the fore-limb. The cleithrum may also serve to strengthen the shoulder-girdle in the scapular-suprascapular region, since it actually meets the scapula, the former being separated from the latter by means of an extremely narrow synovial cavity (Fig. 3, sca). Parker (op. cit.) stated that the "suprascapula" (cleithrum?) sometimes joins the "Praecoracoid" (clavícula). In all the specimens investigated by me the suprascapula or the cleithrum never meets the clavícula (Figures 1 and 2, sc). The smallness of the scapula is characteristic of the *Aglossa* (De Villiers, 1929), and this condition is probably an adaptation to a neotenic feature of aquatic life: a short dorso-ventral body axis. It also occurs in other mainly aquatic anurans, such as in *Bombina*(tor) and *Discoglossus* (Proctor, op. cit., Hsiao, op. cit.), in some *Ranidae* (Hsiao, op. cit.) and in some *Pelobatidae*, e.g. the more

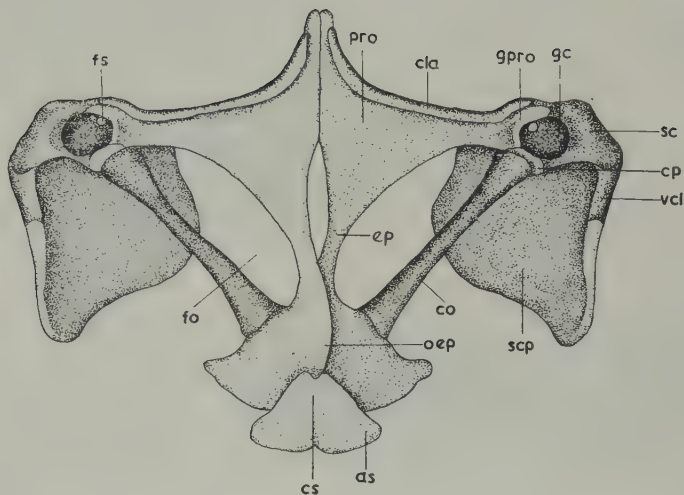


FIG. 2

Graphic reconstruction of the breast-shoulder apparatus of a young postmetamorphic specimen, X 13. Abbreviations as for Fig. 1.

frog-like *Pelodytes* (Proctor, op. cit.). In *Alytes*, which according to Noble (1931) is more terrestrial, the scapula is larger, as is also the case in other typically terrestrial anurans such as in the *Bufo*nidae, in the *Hylidae* and in the rest of the *Pelobatidae* (Proctor, op. cit.).

The glenoid cavity of *Xenopus* is pierced by a foramen, situated in

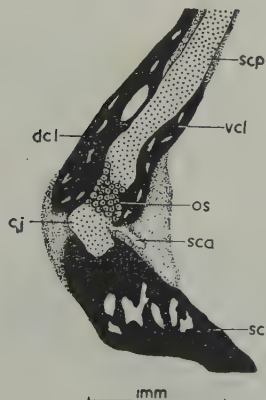


FIG. 3

Transverse section through scapulo-suprascapular hinge to show the ossification of the suprascapula and the synovial cavity between the cleithrum and the scapula. cj: cartilaginous hinge; dcl: dorsal flange of the cleithrum; os: ossification in the suprascapula; sca: synovial cavity in the region of the scapulo-cleithral articulation. Other abbreviations as for previous figures.

that part of the scapula forming the medial wall of the cavity (Fig. 1, 2, 6, fs). Such a glenoid foramen frequently occurs in the *Anura* (Proctor, op. cit., De Vos, op. cit., Braus, 1919). It is lined by the synovial membrane, and in *Xenopus* at least, does not serve for the passage of any nerves or blood-vessels.

According to Braus (1919) the function of the glenoid foramen is to regulate the air pressure in the glenoid cavity during movement of the caput humeri within the cavity. The fact that the synovial membrane is sometimes seen in section to bulge out through the foramen seems to accord well with Braus's point of view.

PROCORACOIDAL CARTILAGE AND CLAVICLE (Fig. 1, 2, pro, cla): The statement by De Villiers (1924) that the procoracoidal cartilages of *Xenopus* may ossify, although the limiting membrane between them and the clavicles remains intact, was doubted by Fuchs (1926 a), who stated that

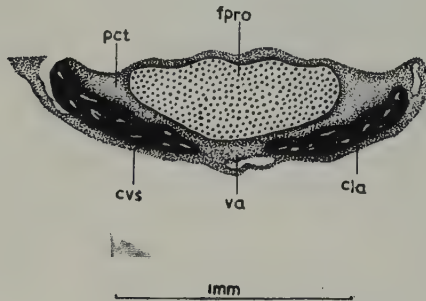


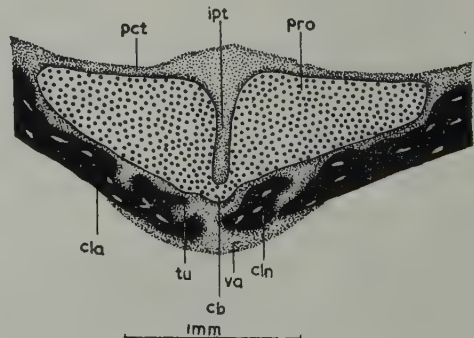
FIG. 4

Transverse section through the anterior parts of the procoracoidal cartilages to show their fused anterior tips. cvs: clavicle-sheath; pct: procoracoidal capsular tissue; va: ventral aponeurosis. Other abbreviations as for previous figures.

such ossifications of the procoracoidal cartilages in *Rana fusca* proceeded only after the membrane had disappeared. De Villiers (1929) thereupon reinvestigated this point, and confirmed his original statement. In all the specimens investigated by me, including the large specimen mentioned above, the limiting membrane between procoracoidal cartilage and investing clavicle is always present, and the antero-medial portions of the procoracoidal cartilages of the large specimen certainly do ossify, or at least show signs of potential ossification (see Fig. 5 b). Marrow-cavities, however, are not developed, although observed by De Villiers (1929) in his specimen. The ossified parts of the procoracoidal cartilages (Fig. 5 b, osf) have the same staining qualities as the other bones. The ossificatory process, however, seems only to effect the matrix of the cartilage, and is therefore intercellular. Islets of cartilaginous tissue (Fig. 5 b, cil) are often seen completely surrounded by bony tissue. In *Xenopus* the microscopic relation of the clavicle to the

FIG 5 a.

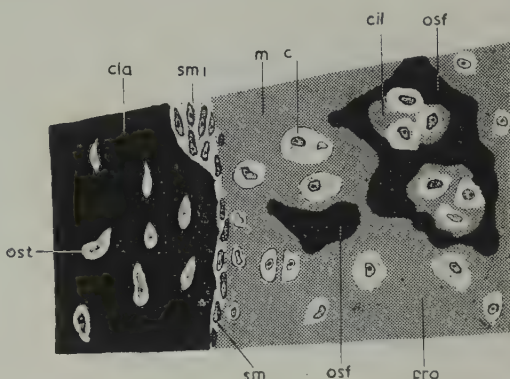
Transverse section through anterior parts of procoracoidal cartilages and clavicles to show clavicular tuberosities, clavicular nodules in the ventral aponeurosis, interprocoracoidal tissue and cartilaginous bridge; cln: clavicular nodule embedded in ventral aponeurosis; ipt: interprocoracoidal tissue; tu: clavicular tuberosity. Other abbreviations as for previous figures.



procoracoidal cartilage is also most interesting. In higher *Anura* the clavicle usually ensheaths the procoracoidal cartilage; typical stages in the progressive ensheathing have been described by Fuchs (1926 a) for *Rana fusca*. In *Xenopus* both the clavicle and the procoracoidal cartilage are well-developed skeletal structures, the latter being appreciably larger than the former (Fig. 1 and 2). The clavicle invests the procoracoidal cartilage ventrally, never extending to the dorsal side of the latter, except at the extreme lateral end of the procoracoidal cartilage, where a narrow flange of the clavicle invests its dorsal surface (Fig. 4, 5). The ventral position of the clavicle is probably

FIG. 5 b

Transverse section through ossified part of procoracoidal cartilage. c: chondroblast; cil: islet of cartilage; m: matrix; osf: ossification in procoracoidal cartilage; ost: osteoblast of clavicle; sm and sml: separating membrane between clavicle and procoracoidal cartilage. Other abbreviations as for previous figures.



a primitive feature as already stated by De Villiers (1929), as the same condition obtains in the *Liopelmidae* (De Vos, op. cit.), in the *Discoglossidae* (De Villiers, 1922), and in some other genera of the *Pipidae*, such as *Hymenochirus* and *Pipa* (De Villiers, 1929). In *Xenopus* the lateral end of the clavicle is so well fused with the scapula that it is impossible to ascertain the line of fusion (see fig. 6). That part of the glenoid cavity formed by the

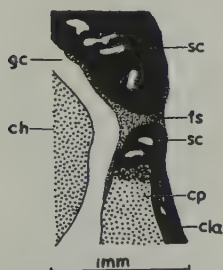


FIG. 6

Transverse section through the glenoid cavity to show the intrascapular position of the glenoid foramen. ch: caput humeri. Other abbreviations as for previous figures.

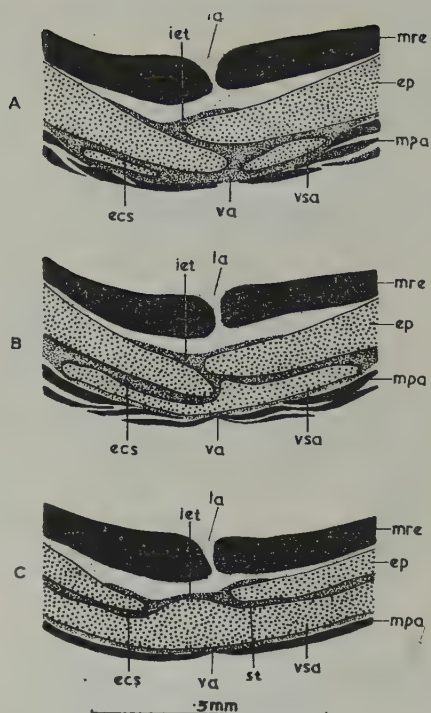
fused scapula and clavicle, is then framed by a single bony element, a condition which frequently occurs in *Anura* (Braus, 1919). This bone, however, should not be compared with the primitive coracoscapula, present in some *Embolomeri* (Romer, 1931) and in the primitive *Liopelmidae* (Romer, 1931, De Vos, op. cit.), as it is not formed by the progressive down-growth of the scapula into the pars procoracoidea of the coracoidal plate. The bony element must be regarded as a secondarily developed, undivided glenoid bone. The clavicle contains no large central marrow cavity, but only a few small cavities,

scattered mainly through the lateral half of the bone. The dorsal surface of the clavicle of the large specimen investigated has an indented appearance since it is studded with fairly large tuberosities (Fig. 5a tu). De Villiers (1929) regarded these tuberosities as local ossifications of the clavicle sheath, and as representing progressive growth of the clavicle towards the procoracoidal cartilage. During this process the limiting membrane between the latter and the clavicles is reduced to a very thin layer. The medial tips of the clavicles and the ventromedial edges of the front parts of the procoracoidal cartilages are seen in section to be embedded in the ventral aponeurosis of the hypaxonic appendicular muscles (see figures 4, 5). The aponeurosis in turn is in direct syndesmotomic continuity with the capsular tissue (which covers the rest of the front parts of the procoracoidal cartilages), with the interprocoracoidal and interepicoracoidal connective tissue, with the clavicle sheath, and indirectly with the linea alba (Fig. 4, 5). The ontogeny of this complex system of connective tissue will be described later. It probably has a double origin, and is essentially skeletogenous. This is proved by the following facts: the median rims of the clavicles of even fully adult specimens show progressive growth towards each other midventrally; the front portions of the procoracoidal cartilages are synchondrotically fused to each other; and scattered islets of cartilage in the interprocoracoidal tissue are often to be found intercalated between the median rims of the procoracoidal cartilages (see figures 4 and 5). It therefore seems that this system of connective tissue, present in the midventral procoracoidal and clavicular part of the shoulder-girdle is capable of giving origin to both membrane bone tissue and to cartilage. It is histologically fairly homogeneous, consisting mainly of fibrous connective tissue. Roggenbau (op. cit.) described an interesting canal system containing blood, in the intercoracoidal tissue of *Rana fusca* and claimed that this tissue probably represents a vestigial interclavicula. De Villiers (1929) also described and figured such a canal system in the capsular tissue of *Xenopus*. He maintained, however, that the canals do not contain blood, and that the fibres and nuclei are arranged concentrically round these canals. It was not possible to demonstrate the canal system in any specimen investigated, but I do agree with De Villiers that no histological change in the interprocoracoidal or capsular tissue of *Xenopus* shows any signs of its being a possible vestige of membrane bone preformed in connective tissue, however true this may be for *Rana fusca*. The system of connective tissue described above, serves to attach the two procoracoidal halves of the shoulder-girdle firmly to each other, that region of the shoulder-girdle thus being both anatomically as well as functionally firmisternal.

PROCESSUS EPICORACOIDEI: These structures are articulated on the arciferous principle (Fig. 1, 2, ep, oep), as already stated by De Villiers (1922, 1924, 1929), and are rather loosely attached to each other midventrally by means of a loose network of fibres, permitting some movement between the processus epicoracoidei. Like the interprocoracoidal tissue, the interepicoracoidal tissue is connected with the ventral aponeurosis and with the linea alba (see Figure 7). This system of connective tissue likewise shows skeletogenous activities since it forms the mother-tissue of certain parts of the sternum, the development of which will be discussed later. It should be mentioned at this point, that both Fuchs (1926 b) and De Villiers (1929) had already commented on the potential skeletogenous nature of the interprocoracoidal and

FIG. 7

A series of sections through the epicoraco-sternal region of the breast-shoulder apparatus of an old post-metamorphic individual. A through the paired anterior part of the sternum. B through the region a few sections posterior to A. C through the corpus and lateral wings of the sternum. ecs: epicoraco-sternal tissue; iet: interepicoracoidal tissue; la: linea alba; mpa: portio abdominalis muscoli pectoralis; mre: m. rectus abdominis; vsa: ventral sternal element constituting the adult sternum. Other abbreviations as for previous figures.



interepicoracoidal tissue. De Villiers regarded this tissue as a linea alba derivative, while Fuchs (1926 b) considered it together with the sternum of *Anura* as being originally of costal origin, a point of view which is certainly not supported by ontogenetic evidence. Parker (1868) and Fürbringer (1873) observed a discontinuity of the processûs epicoracoidei in *Xenopus*, this being denied by De Villiers (1924, 1929) and by all subsequent workers. In none of the specimens which I investigated did a single processûs epicoracoideus show any signs of being discontinuous, although they are sometimes extremely thin. They flatten out posteriorly, these flanges being firmly attached syndesmotically to the dorsal surface of the sternum in the adult condition.

STERNUM: In *Xenopus* the sternum is entirely cartilaginous, as in primitive *Anura*. It consists of a corpus sterni situated midventrally, and two broad, thin lateral wings, embedded in between the m. rectus abdominis and the portio abdominalis muscoli pectoralis (Fig. 1, 2). The original paired condition of the sternum is easily observable, as the corpus sterni has an extremely shallow groove on its antero-dorsal surface. The lateral wings are by no means constant in form. In large adult specimens which I investigated, the wings are greatly extended laterally, the sternum then being broader than the combined width of the posterior flat portions of the processûs epicoracoidei (Fig. 1). But in younger ones the wings are much smaller and the flanges of the processûs epicoracoidei are broader than the sternum (Fig. 2). Its posterior edge is sometimes fairly deeply notched in the middle line. Judging from

investigations on a large number of larval, young and adult specimens, it seems that the presence of sternal pouches for the reception of the posterior rims of the processûs epicoracoidei, is not a constant feature in *Xenopus*. Sternal pouches are probably confined to larval and small postmetamorphic specimens (see figure 8). In older postmetamorphic and in adult individuals

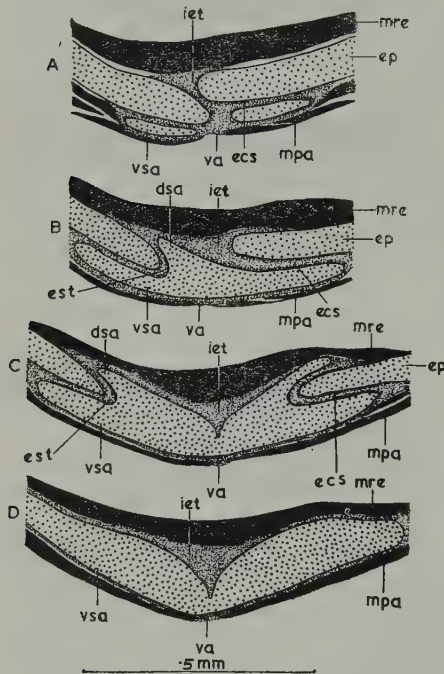


FIG. 8

A series of transverse sections through the epicoraco-sternal region of a small postmetamorphic individual. A through the paired anterior part of the sternum. B through the anterior part of the right sternal pouch. C through the sternal pouch region. D through the posterior part of the sternum. dsa: dorsal sternal element constituting the roof of the sternal pouch; est: sternal pouch filled with epicoraco-sternal tissue. Other abbreviations as for previous figures.

the sternal pouches usually have no dorsal walls but form sternal fossae, which in section appear as slight depressions on the dorsal antero-lateral parts of the corpus sterni (Fig. 7, stf). The posterior rims of the processûs epicoracoidei are firmly attached to these fossae by means of the dense, elastic epicoraco-sternal tissue. Even in larval or young individuals the sternal pouches of the right and left sides are not equally developed, the right sometimes being better developed than the left (Fig. 21). This phenomenon can probably be explained on mechanical grounds. As the right processus epicoracoideus generally overlaps the left one, and is thus situated ventrally to the latter, it is obvious that the right sternal pouch will be better developed than the left, in order to prevent too much displacement of the processûs epicoracoidei. In *Pipa* the dorsal elements are entirely absent, even in developmental stages (De Villiers, 1929), while in *Hymenochirus* only vestiges of the dorsal elements are present, the sternum having fused with the processûs epicoracoidei (De Villiers, 1929). The total or potential loss of the dorsal elements in the *Aglossa* is quite remarkable, as they are present in the *Liopelmidae* (De Vos, op. cit.) and in the *Discoglossidae* (De Villiers, 1922). The aglossal condition is probably due to an increasing loss of motion in the epicoraco-sternal and

mutual epicoracoidal articulation, as the aglossal shoulder-girdle shows an increasing tendency towards firmisterny, a condition already attained by *Hymenochirus*, while *Pipa* is already functionally firmisternal, although anatomically still arcifero-firmisternal (De Villiers, 1929). Only in *Xenopus* are the processûs epicoracoidei still capable of movement. The procoracoidal cartilages are anatomically and functionally firmisternal. This progressive tendency towards firmisterny in the aglossal genera mentioned above probably does not form a "phylogenetic" series, as already pointed out by De Villiers (1929), since the present distribution of the group does not support such an assumption. It is rather to be regarded as an instance of convergence, and is probably due to the aquatic habit of life (see later).

EPISTERNUM: This element is phylogenetically regarded as the most recent structure in the anuran breast-shoulder apparatus, and it is usually better developed in the *Firmisternia* than in the *Arcifera*. The absence of an episternum is a characteristic feature of the more primitive anurans, such as the *Liopelmidæ* (De Vos, op. cit.), and of the *Aglossa*. It is very small in the *Discoglossidæ* (*Bombinator*: Braus 1919, De Villiers, 1922). The latter author regarded the absence of an episternum in the *Aglossa* as a primitive feature. For a detailed account of the development of the episternum in other anurans the reader is referred to the historical introduction.

THE DEVELOPMENT OF THE SHOULDER-GIRDLE

The development of the shoulder-girdle and of the sternum will be dealt with separately, as the latter develops late in ontogeny, when the former has already attained an advanced state of development. Since the ontogeny and morphology of the sternum, and especially of the anuran sternum, have been frequent objects of research in the past, the ontogeny of the girdle itself and its mother-tissue have been somewhat neglected. As was stated in the historical introduction, the vertebrate skeleton, apart from chitinous or calcareous derivatives of the ectoderm and the enamel of the teeth, is of mesodermal origin. Ruge (1902), De Villiers (1926) and Engler (op. cit.) state that the limb-bud tissue is of mesenchymatous origin, and Goodrich (op. cit.) maintains that the girdle and limb musculature have a myotomic origin, arising as cell proliferations from the ventral ends of the myotomes.

The following description of the development of the shoulder-girdle is based on the careful study of a large number of metamorphic and post-metamorphic larvae. The development of the fenestra and membrana obturatoria is treated in the light of the investigations of Fuchs (1927) on *Rana fusca* and of Braus (1909) and Nauck (op. cit.) on *Bombina(tor)* and *Alytes*. The observations on the origin, development and skeletogenous activities of the ventral aponeurosis are quite new, as this structure probably has been overlooked somewhat by all previous workers.

Stage A: The limb-bud first appears in section as a small, thickened patch of blastematous tissue, partly projecting into a small cavity, the atrium (Fig. 9). The latter cavity is situated in the lateral part of the body wall immediately dorsal to the posterior part of the gill region and lateral to the posterior part of the pronephros anlage. The atrium is of course lined with ectoderm, which is continuous with a row of large cells covering the limb-bud

laterally, and representing the ectoderm of the latter (Fig. 9, ect). That part of the body wall in the immediate vicinity of the limb-bud is characterised by the thickened appearance of the somatopleuric coelomic epithelium and of the epidermis. It does not follow, however, that any cells are proliferated from them, since it is usually accepted that the ectoderm and the somatopleuric coelomic epithelium are not fasciogenic, although it is stated by some histologists (e.g. Bremer and Weatherford, 1944) that the somatic mesoderm can give rise to mesenchyme. The ectoderm, however, apparently does not contribute to the limb-bud tissue. This view is also supported by Rotman's observations (1931). Working along transplantational lines on urodeles,

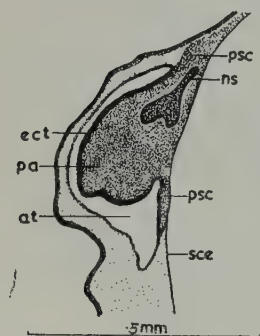


FIG. 9

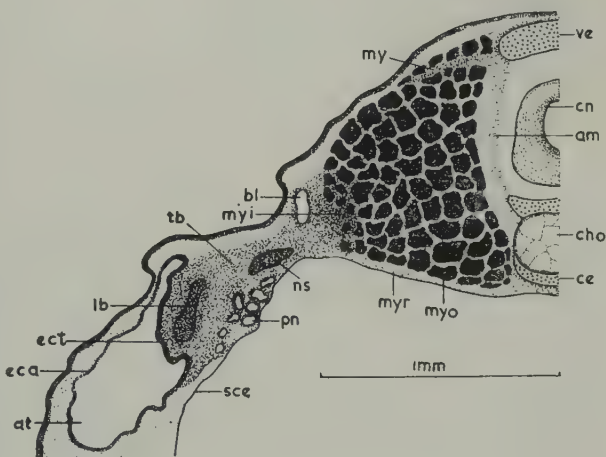
Transverse section through limb-bud of the youngest larva investigated. at: atrium; ect: ectoderm of the limb-bud; ns: limb-bud nerve; pa: pars appendicularis; psc: pars scapulo-coracoidea; sce: somatopleuric coelomic epithelium.

Rotman came to the conclusion that the urodelan ectoderm does not contribute any material to the limb-bud tissue. De Villiers (1926) maintains that the thickenings, described above, "arise in response to the greater strain exacted upon these confining epitheliums by the growing anlage between them." Even at this early stage of development at least two regions are discernible in the limb-bud: (a) a portion bulging slightly into the atrium, and obviously representing the front leg; this may be called the pars appendicularis of the limb-bud (Fig. 9, pa); (b) a vertically disposed platelike part, which may be called the pars scapulo-coracoidea of the limb-bud, occupying a position nearly at right angles to the former, and representing the earliest anlage of the girdle (Fig. 9, psc). That part of the axial mesenchyme situated lateral to the spinal chord is still unchondrified, and the myocommata between consecutive myotomes are clearly visible as distinct strands of connective tissue, staining blue with azan, and traversing the myotomes obliquely (Fig. 10, my, myi). Thus in following the sections backwards, the myocommata, being curved, always appear to shift gradually from the dorso-medial to the ventro-lateral aspects of the myotomes. At the level of the latter parts of the myotomes, situated dorsally to the limb-bud region, the histological structure of the myocommata can be seen more clearly; they consist of blastemata tissue histologically identical with the axial mesenchyme. These ventro-lateral parts of the myocommata, which are of course continuous with the axial mesenchyme, are in turn continuous with the limb-bud tissue by means of a patch of blastemata tissue situated between the cutis laterally and the somatopleuric coelomic epithelium medially, and stretching from the ventro-lateral margins of the myotomes to the limb-bud (Fig. 10, tb). Histologically the axial mesenchyme, the myocommata and the patch of tissue described above are quite similar, consisting as they do

mainly of large elongated nuclei with sparsely distributed cytoplasmic strands. The nuclei of the limb-bud tissue are more rounded, this probably being due to the more compact structure of the latter. No cell differentiation of any kind has yet taken place. From this description it is reasonable to infer that the limb-bud tissue is of mesenchymatous origin, and that the growth of the mesenchyme from the axial mass takes place through and along the myocommata, a point of view supported by the fact that the long axes of the nuclei of the myocommata and of the patch of tissue described above always point in a ventral direction, that is, in the direction of the limb-bud. This circumstance probably points to the active growth of mesenchyme from the axial mesenchyme along the myocommata to the limb-bud. It seems as though there might be yet another route of growth for the mesenchyme: between the ventral border of the myotomes and the somatic coelomic epithelium, as elongated connective tissue nuclei are also present between these two structures (Fig. 10, myr). Incidentally this is the same route later to be followed by the limb-bud nerve. The chorda dorsalis is a well-developed structure, consisting in section of a few, large vacuolated cells with the nuclei confined to the inner surface of the notochordal sheath, surrounding the cellular part of the chorda (Fig. 10, cho). The centra of the vertebrae are already chondrified

FIG. 10

Transverse section through the myotome and limb-bud region to show the migratory routes of the mesenchyme. am: unchondrified part of axial mesenchyme; bl: blood-vessel; ce: centrum; cho: chorda dorsalis; cn: dorsal nerve chord; eca: ectoderm lining the atrium; lb: limb-bud; my: dorsal part of myocomma; myi: ventrolateral part of myocomma filled with dense mesenchymatous tissue; myo: myotome; myr: space between ventral border of myotome and somatopleuric coelomic epithelium; pn: pronephros; tb: thickened blastematos patch of tissue connecting the limb-bud and myocommatous tissues; ve: Dorsal part of vertebra.



subchordally. In this stage the ventral margins of the two halves of the *m. rectus abdominis* are widely separated from each other, and the linea alba is an extremely thin sheet of connective tissue continuous with the myocommata. It is fairly certain that the myocommatous tissue of the *m. rectus abdominis* and the linea alba tissue represent mesenchyme, probably derived from the axial mesenchyme (De Villiers, 1925). The latter, however, is probably not the only source of the mesenchyme present in the lateral and ventral abdominal wall, since it is stated by some histologists (e.g. Bremer and Weatherford op. cit.) that mesenchyme can also be proliferated from the somites (apart from

the latter giving origin to the axial mesenchyme), and from the somatic mesoderm. According to some workers skeletogenous mesenchyme of the visceral arch skeleton is derived from the neural crest.

Stage B: As in the previous stage cell-differentiation has not yet taken place. The pars appendicularis of the limb-bud anlage has grown considerably larger and now points downwards into the atrium, while the pars scapulo-coracoidea has likewise increased in size, and is divided into two parts by the limb-bud nerve or brachial plexus. The latter has been formed by the fusion of two nerve roots passing from two consecutive spinal ganglia to the limb-bud. The brachial plexus gives origin to four nerve branches, and judging by the positions occupied by these nerves in later stages, it is possible to distinguish with certainty the main regions into which the limb-bud will later develop (Fig. 11, nh, npc, nps). That part of the latter lying in the vicinity

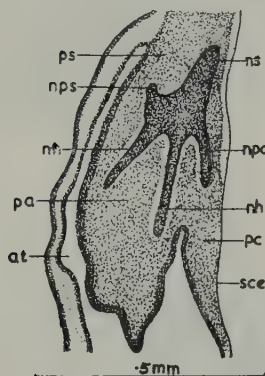


FIG. 11

Transverse section to show the brachial plexus and its four nerves, and the main regions of the limb-bud. nh: nerves to front leg; npc: n. supracoracoideus to pars coracoidea; nps: nerve to pars scapularis; ns: brachial plexus; pc: pars coracoidea; ps: pars scapularis.

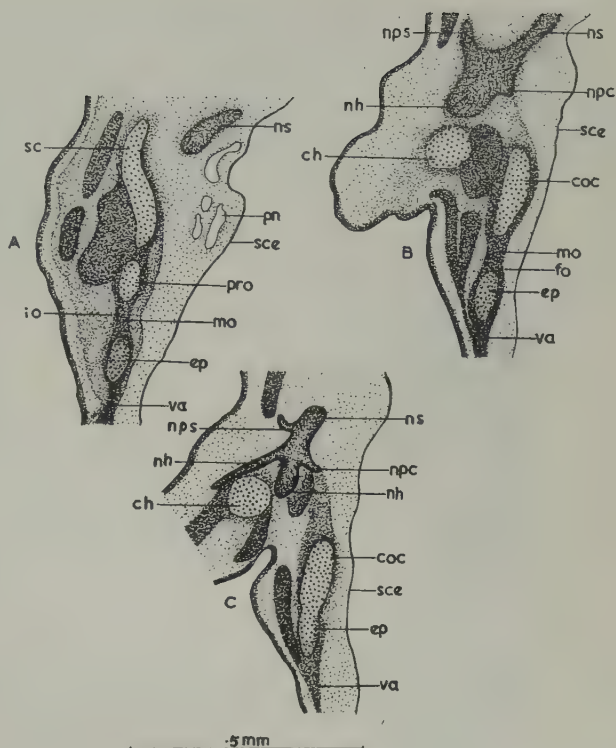
Other abbreviations as for previous figures.

of the dorsal nerve branch (nps) represents the pars scapularis (ps), since this nerve in later stages innervates the scapular region of the girdle and its associated musculature. The part lying in the vicinity of the ventral nerve branch (npc) (n. supra-coracoideus of Engler and various other authors) constitutes the future pars coracoidea (pc) of the scapulo-coracoidal plate, since this branch in later stages passes through the antero-dorsal corner of the fenestra obturatoria to innervate the supra-coracoideus muscles of the pars coracoidea. The two middle nerve branches (nh, nh) pass to the limb-anlage (pa) and innervate the limb musculature. In this stage the limb-bud tissue therefore consists of three parts: the pars appendicularis, the pars scapularis partis scapulo-coracoideae and the pars coracoidea partis scapulo-coracoideae.

Stage C: The limb-bud tissue has now undergone remarkable changes, as cell-differentiation has set in; certain parts of the mesodermal core of the limb-bud are chondrified, while the rest is still densely blastematos or procartilaginous (Fig. 12A, B. C). The migration of axial mesenchyme through the myocommata is even more pronounced in this stage, as condensed patches of blastematos tissue are always present ventral to those parts of the myocommata immediately dorsal to the limb-bud region. Such patches thin out considerably in the regions between consecutive myocommata, and are entirely absent anterior and posterior to the limb-bud region. The girdle

FIG. 12

Three sections through the limb-bud region to show the development of the processus epicoracoideus and the formation of the fenestra obturatoria and the membrana obturatoria. A through the scapula, procoracoidal cartilage and procartilaginous part of processus epicoracoideus. B through the caput humeri, coracoidal cartilage and procartilaginous part of the processus epicoracoideus. C through the cartilaginous part of the processus epicoracoideus fused with the coracoidal cartilage. coc: coracoidal cartilage; io: incisura obturatoria; mo: membrana obturatoria covering the incisura obturatoria. Other abbreviations as for previous figures.



and limb musculature appear for the first time as distinct patches of dense blastematous tissue. The caput humeri (Fig. 12 B, ch) is chondrified, although it is still in syndesmotomic continuity with the shoulder-girdle anlage, and no synovial cavity has yet developed. The pars scapularis is chondrified and is already faintly divided into scapular and suprascapular portions, the latter appearing as a small dorso-laterally directed process of the former. The platelike pars coracoidea chondrifies simultaneously in two centres, giving origin to the coracoidal and procoracoidal cartilages (Fig. 12, coc, pro). The processus epicoracoideus (ep) first appears in section as a procartilaginous bar separated from the procoracoidal cartilage by means of dense blastematous tissue. Further back it gradually becomes cartilaginous, and is in synchondrotic continuity with the ventral end of the coracoidal cartilage. The processus epicoracoideus therefore appears to be a process of the coracoidal cartilage, for its anterior end has not yet fused with the procoracoidal cartilage. The space surrounded by the coracoidal cartilage (later the os coracoideum or coracoid) posteriorly, the procoracoidal cartilage anteriorly and the processus epicoracoideus ventrally, which may be called the incisura obturatoria (io), is therefore not yet entirely closed. It is still open in the region of the procoracoidal cartilage, and is entirely filled up with dense unchondrified tissue of the pars coracoidea (mo), except for a fairly large foramen in its anterodorsal corner, through which the n. supratoracoideus passes to the laterally situated hypaxonic appendicular musculature. Of very great importance

is a patch of blastematos tissue (va) continuous with the ventral margins of the procoracoidal cartilage and of the processus epicoracoideus. It tapers in a ventral direction to a thin strand of connective tissue continuous with the inscriptions of the m. rectus abdominis. Even at this early stage of development it serves as a point of insertion for the hypaxonic appendicular musculature, and is to be regarded as unchondrified tissue of the pars coracoidea; it is undoubtedly the mother tissue of the ventral aponeurosis. At this stage the linea alba is still a broad stretch of connective tissue binding the two halves of the m. rectus abdominis, which are still widely separated from each other ventrally.

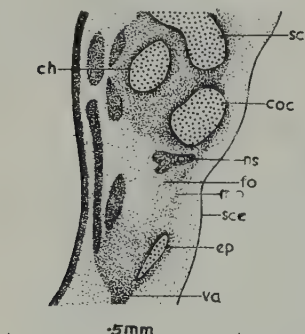


FIG. 13

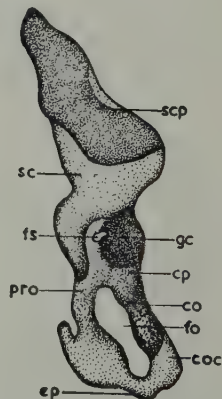
Transverse section through the limb-bud region to show the reduction of the membrana obturatoria and the enlargement of the fenestra obturatoria.

Abbreviations as for previous figures.

Stage D: This stage is characterised by the advanced degree of chondrification attained by certain parts of the shoulder-girdle, the commencement of perichondral ossification of the humerus and the coracoidal cartilage, and the chondrification of the ribs in the myocommata of the myotomes (see fig. 14). The suprascapula, though well chondrified, is still very small

FIG. 14

Graphic reconstruction of the left half of the shoulder-girdle (stage D). X 33. Abbreviations as for figures 1 and 2.



and points in a lateral direction. The incisura obturatoria is now to be regarded as a fenestra obturatoria (Fig. 13, fo), for the processus epicoracoideus is entirely cartilaginous and has fused with the postero-ventral margin of the procoracoidal cartilage. The fenestra obturatoria is covered by a thin sheet of connective tissue, the membrana obturatoria (mo), which in the

previous stage had a more dense blastematos appearance. It is to be regarded as unchondrified blastematos tissue resulting from the reduction of the pars coracoidea. The mother tissue of the ventral aponeurosis stretches further downwards than in the previous stage, and actually lies partially ventro-lateral to the dorsal margin of the m. rectus abdominis. The caput humeri is still in syndesmotic continuity with the shoulder-girdle, but the outlines of the glenoid cavity can already be distinguished.

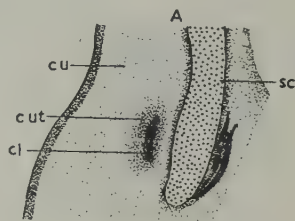
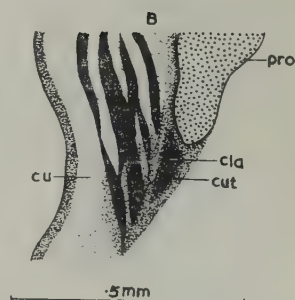


FIG. 15

Transverse sections of stage E to show the development of the cleithrum and of the clavicle. cu: cutis; cut: cell-thickening in the cutis. Other abbreviations as for previous figures.



Stage E: Commencement of the ossification of the membrane bones, and the formation of the synovial cavity are characteristic features of this stage (see fig. 16). The scapula (Fig. 16, sc) is still entirely cartilaginous, while the coracoidal cartilage is partly ossified perichondrally to form the coracoid (co). Like the latter, the humerus is also ossified perichondrally. Marrow-cavities, however, are absent in both structures. The suprascapula (scp) is considerably larger than in the previous stage, and is invested on its outer aspect by an extremely small cleithrum (cl). In section the latter first appears as a small patch of osseous tissue, which stains deep blue with azan, and is embedded in a much larger patch of thickened connective tissue (Fig. 15 A). Although cuticular connective tissue and thinly dispersed mesenchymatous tissue are histologically not distinguishable from each other, the anlage of the cleithrum can only be regarded as a derivative of the cutis, since it occupies a subepidermal position, always occupied morphogenetically by Rabl's "Hautfaserblatt" of the myotome. The cleithrum is certainly not a mesenchymatous derivative, since it is not preformed in cartilage as all osseous derivatives of the mesenchyme are, and since the only unchondrified mesenchymatous material in the vicinity of the cleithrum, the suprascapular

perichondrium, remains totally intact. The clavicle (Fig. 15 B, cla) likewise first appears as an osseous nodule embedded in a dense patch of cuticular tissue lying ventrally to the glenoid part of the procoracoidal cartilage, and in direct continuity with the general cutis. The posterior part of the clavicular anlage is already covered laterally by the hypaxonic musculature, and in this region the anlage is therefore not in direct continuity with the cutis, this part of the anlage being formed in an island of cuticular tissue secondarily separated from the main cutis. It is therefore quite evident that both the cleithrum and the clavicle are cuticular derivatives, as all ossa investientia are, and that the tissue covering these bones in later stages and in the adult condition is in reality a formative derivative of the cutis and known histogenetically as the periosteum. The fenestra obturatoria is considerably larger than in the previous stage, the foramen obturatorium only occupying a small portion of

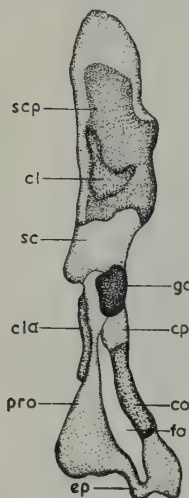


FIG. 16

Graphic reconstruction of the left half of the shoulder-girdle (stage E), to show the relations of the cleithrum to the suprascapula and of the clavicle to the procoracoidal cartilage. X 33. Abbreviations as for figures 1 and 2.

its antero-dorsal part. The linea alba is still a very broad stretch of connective tissue, since the ventral margins of the m. rectus abdominis are still widely separated from each other, while the mother tissue of the ventral aponeurosis occupies essentially the same position as in the previous stage.

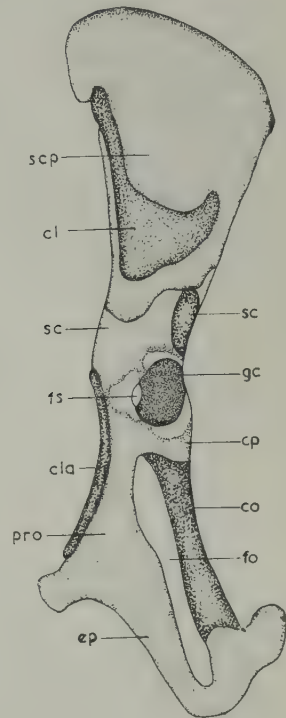
Stage F (Fig. 17): A distinct constriction is now present between the dorsal tip of the scapula and the ventral end of the suprascapula, and it obviously represents the future joint between these two structures. The suprascapula (scp) is now a large, curved plate of cartilage covering laterally a considerable part of the myotomes. The scapula (sc) is partly ossified perichondrally, but marrow-cavities are still absent. Both the cleithrum (cl) and the clavicle (cla) are much larger than in the previous stage, neither of them possessing any marrow-cavities. The ventral margins of the procoracoidal cartilages, the processus epicoracoidei and the m. rectus abdominis are still widely separated, in spite of the advanced degree of development. This condition can be easily explained, as the spirally twisted intestine in this stage has attained its maximum size. The mother tissue of the ventral aponeurosis stretches far downwards along the latero-ventral margins of

the m. rectus abdominis, and in the region of the processus epicoracoideus it is separated from the latter process by means of a clear space simulating a synovial cavity. This space indicates that movement of some kind or other of the processus epicoracoideus is possible, since in the adult condition, in which the processus epicoracoidei are certainly capable of a sliding movement over each other, the ventral aponeurosis and the interepicoracoidal tissue are also separated from them by similar clear spaces. It should also be mentioned that in this stage the first traces of the sternum are to be seen.

FIG. 17

Graphic reconstruction of the left half of the shoulder-girdle (stage F) to show the extent and relations of the membrane bones to the rest of the shoulder-girdle. X 22.

Abbreviations as for figures 1 and 2.



Stage G: The girdle now has quite an adult appearance, and the procoracoidal cartilages and processus epicoracoidei are approaching each other midventrally; the spirally twisted gut has undergone considerable reduction. The processus epicoracoidei, however, do not yet overlap. The coracoid now contains a large central marrow-cavity and also a few smaller cavities, but the scapula is still solid. The clavicle is still quite small; it covers only a small part of the procoracoidal cartilage, and is not yet fused with the scapula, but simply abuts against its ventral margin. The cleithrum, on the contrary, is already an extensive bone, covering a large part of the lateral aspect of the suprascapula, and containing several marrow-cavities, some of them opening to the exterior. The cleithrum is, however, still widely separated from the dorsal end of the scapula. A very important change is that the right and left anlagen of the ventral aponeurosis have fused with each other mid-

ventrally, and that this continuous stretch of connective tissue is in direct continuity with the linea alba, which is now much narrower than in the previous stage, for the ventral ends of the m. rectus abdominis have considerably approached each other (see figs. 18 and 19). The connective tissue constituting the linea alba is much denser than in the previous stage, especially in the region of the posterior parts of the processûs epicoracoidei. The glenoid foramen described in the adult condition first appears in stage C as a distinct cleft covered by blastematos tissue, and situated between the pars scapularis and the pars coracoidea. In later stages it is situated between the ventral margin of the scapula and the dorsal part of the cartilago paraglenoidalis. Of the adult specimen described in the previous chapter, it was stated that this foramen is situated in the scapula (Fig. 6, fo). This intrascapular position is certainly secondary, and is the result of the progressive downgrowth into, or invasion of, the cartilago paraglenoidalis by the scapula. The proof that this is actually so is that in the adult condition the cartilago paraglenoidalis (Fig. 6, cp) is only a small piece of cartilage lining a part of the glenoid cavity and separating the coracoid from the scapula. The synovial membrane lining the glenoid cavity, and the fibrous glenoid capsular tissue are both mesenchymatous derivatives (Cf. Hamilton, Boyd and Mossman (1945), and Maximow and Bloom (1944)).

In conclusion certain important points relating to the development of the shoulder-girdle will be discussed in further detail. From the above description of the development of the cleithrum and the clavacula it is quite evident that both are derivatives of the cutis, as are all ossa investientia. Braus (1904) first suspected that the cleithrum is a membrane bone, and confirmed it in his later works (1909, 1919). It should also be mentioned that Fuchs (1922) and De Villiers (1922) independently came to the same conclusion as Braus. Various criteria, which will not be discussed in detail here, were set up for membrane bones by Fuchs (1922) and Braus (1919). These criteria, however, are not always to be trusted, except perhaps as corroborative evidence for the only safe criterion, the ontogenetic one, as repeatedly stressed by De Villiers (1922, 1925, 1926, 1929).

As stated in the historical introduction, two different theories were set up by various authors for the origin of the fenestra obturatoria present in the ventral half of the Amphibian shoulder-girdle. Fuchs (1927) regarded it as a primary fenestra ("Sprossungsfenster"), situated anterior to the pars coracoidea, and surrounded by the coracoid, procoracoidal cartilage and the processus epicoracoideus. The coracoid, forming the postero-lateral boundary of the fenestra obturatoria, is regarded as the only derivative of the pars coracoidea, while the processûs epicoracoideus is a forwardly directed process of the coracoid (or its cartilaginous homologue). Fuchs also regards the procoracoidal cartilage as a ventrally directed process of the pars scapularis, and therefore not belonging to the pars coracoidea. A primary fenestra obturatoria is therefore not situated in the pars coracoidea, but anterior to it, since the only derivative of the pars coracoidea, the coracoid, forms the latero-posterior boundary of the fenestra. The membrana obturatoria covering the primary fenestra is regarded as a secondary membrane ("fibrogene Membran"), since it develops late in ontogeny from fibrous connective tissue not belonging to the shoulder-girdle. According to Braus (1909) and Nauck (op. cit.) the fenestra obturatoria in *Bombina(tor)* and *Alytes* arise very

early in ontogeny as a foramen pro nervo supracoracoideo, situated in the antero-dorsal part of the blastematous or procartilaginous pars coracoidea. This foramen later enlarges to form the large fenestra obturatoria present in the adult condition. The coracoid, procoracoidal cartilage and processus epicoracoideus originate as separate chondrifications in the pars coracoidea. In *Xenopus* the fenestra obturatoria is formed in much the same way. In early stages of development (e.g. stages B and C) the blastematous and in later stages the procartilaginous pars coracoidea is pierced by the foramen, described above, for the transit of the n. supracoracoideus. The coracoid and procoracoidal cartilages subsequently chondrify simultaneously in the pars coracoidea, posteriorly and anteriorly to this foramen respectively, thereby enclosing the latter and a considerable part of the unchondrified pars coracoidea in a space between them — the incisura obturatoria. This is later closed ventrally to form the fenestra obturatoria by the development of the processus epicoracoideus, which in *Xenopus* is to be regarded as a process of the coracoid. The foramen pro nervo supracoracoideo is therefore also incorporated in the fenestra obturatoria, but it is not responsible for the further enlargement of the latter, as this is brought about by the reduction of the covering blastematous tissue to form a thin connective tissue membrane, the membrana obturatoria, entirely absent in the adult condition. The fenestra and membrana obturatoria in *Xenopus*, therefore, actually conform to a secondary fenestra ("Reduktionsfenster" of Fuchs) and a primary membrane ("Reduktionsmembran" of Fuchs) respectively, both of which, according to this author, are present in lizards. It certainly is not a primary fenestra, since it originates in, and not anterior to, the pars coracoidea, since the latter gives rise to both the coracoid and procoracoidal cartilage, and not to the coracoid alone, as is claimed by Fuchs for *Rana*. The processus epicoracoideus is a process of the cartilago coracoidea (which later ossifies to form the coracoid) as in *Rana* and not a separate chondrification of the pars coracoidea as described for *Alytes* by Nauck.

The ontogeny of the tissues constituting the complex system of connective tissue present between the ventral halves of the girdle has already been discussed by De Villiers (1929) and Fuchs (1926 b). The latter maintains that the episternum, the interprocoracoidal and interepicoracoidal tissues and the sternum represent the remains of a once large skeletal structure ("Ursternum") intercalated between the ventral halves of the girdle. The anterior part of the "Ursternum" (the episternum) he considers to be of zonal origin, the rest, including the sternum, being of costal origin, although this conclusion can no longer be proved by ontogenetic evidence. De Villiers (1929) maintains that the procoracoidal capsular tissue, the interprocoracoidal and interepicoracoidal tissues, and the epicoraco-sternal tissue are of linea alba origin, arising as cell-proliferations along the ventral margins of the m. rectus abdominis, and that a part of this tissue also constitutes the mother tissue of the sternum. The same author regards that part of the tissue which will give rise to the clavicle sheath as a cuticular derivative. But he says nothing about the origin of the tissue forming the ventral aponeurosis. The following discussion will deal with the ontogeny and skeletogenous activities of the complex system of connective tissue entities described above. The development of the sternum, however, which is an

integral part of the skeletogenous activities of these tissues, will be discussed in the next chapter.

In *Xenopus* the tissues in question are not derivatives of the ribs as such, but the tissue forming the ventral aponeurosis is undoubtedly of mesenchymatous origin, and is in direct syndesmotic continuity with the ventral margin of the blastematos pars coracoidea. It is therefore a derivative of the limb-bud tissue, and since the latter is probably a derivative of the axial mesenchyme, it is no more than logical to regard the ventral aponeurosis, the free appendicular skeleton and the girdle as being possibly of mesenchymatous origin as well. The mesenchyme forming the latter two structures chondrifies (or ossifies as the case may be); the mesenchyme round the ventral margin of the girdle changes from undifferentiated mesenchymal tissue to functional binding tissue, as it has a binding instead of a skeletal function, and constitutes the mother tissue of the ventral aponeurosis. The latter stretches midventrally from the anterior to the posterior part of the shoulder-girdle, and forms a kind of pseudolinea alba, situated externally to the shoulder-girdle, the actual linea alba being situated internally to the ventral halves of the girdle (see fig. 20). In old premetamorphic specimens the ventral aponeurosis is in direct continuity with the linea alba for the whole length of the shoulder-girdle, and in the sternal region its tissue is somewhat thickened. The same applies to the linea alba. In this region in postmetamorphic specimens the ventral aponeurosis is in direct continuity with the linea alba only through the interprocoracoidal and interepicoracoidal tissues and becomes more ligamentous serving primarily as the point of insertion for the hypaxonic limb and girdle musculature. Incidentally, it also forms the mother tissue for certain parts of the sternum.

The interepicoracoidal and epicoraco-sternal tissues are to be regarded as derivatives of the ventral aponeurosis and of the linea alba. In the posterior epicoracoidal or sternal region the interepicoracoidal tissue is greatly thickened and broadly continuous with the ventral aponeurosis and with the linea alba (Fig. 20). In the sternal region, therefore, there is a concentration of connective tissue, originating from the latter two connective tissue entities. From this interepicoracoidal concentration of tissue the dorsal parts of the sternum are formed, while the epicoraco-sternal tissue must be regarded as unchondrified interepicoracoidal tissue of the sternal region. Anterior to this region the interepicoracoidal tissue is only a thin strip of connective tissue, binding the processûs epicoracoidei loosely to each other, and it is anteriorly continuous with the interprocoracoidal tissue.

The interprocoracoidal tissue binding the procoracoidal cartilages (Fig. 5, ipt), and the capsular tissue (pct) covering the antero-lateral and antero-dorsal parts of procoracoidal cartilages also have a double origin: they arise as cell proliferations from the linea alba and from the ventral aponeurosis. In large postmetamorphic and adult specimens the continuity of the capsular and interprocoracoidal tissues with the linea alba is interrupted, the latter being situated much deeper than the former. The ventral aponeurosis and the two connective tissue entities in question show skeletogenous activities since scattered nodules of cartilage are often found interprocoracoidally, and the medio-ventral margins of the front parts of the procoracoidal cartilages are connected to each other, in old specimens, by means of a cartilaginous bridge (Fig. 5, cb). This bridge is a chondrification of the ventral part of the capsular

tissue and of the ventral aponeurosis. In very large specimens such chondrifications have proceeded so far that the entire anterior interprocoracoidal tissue is affected by the chondrification, so that the anterior parts of the procoracoidal cartilages are in actual synchondrosis (see fig. 4).

In the previous chapter it was stated that the dorsal rims of the clavicles possess fairly large tuberosities (Fig. 5, tu), and that their median rims show progressive growth towards each other midventrally. Since these growing median rims of the clavicles, like the medio-ventral rims of the procoracoids, are embedded in the ventral aponeurosis it is evident that this structure can give rise to cartilage and to membrane bone. It is of course histologically quite impossible to distinguish cuticular elements capable of giving origin to membrane bone tissue in the ventral aponeurosis, but that such elements do occur is obvious, otherwise the progressive growth of the clavicles cannot be accounted for. It seems logical to conclude that formative cuticular cells are proliferated from the clavicular periosteum, that these cells become embedded in the ventral aponeurosis, and that it is because of them that the ventral aponeurosis, which is a mesenchymatous derivative, can give origin to membrane bone tissue. This point of view is supported by the development of the tuberosities described above, which are to be considered as local ossifications of the clavicle sheath, i.e. of the clavicular periosteum, since the latter is the only unossified cuticular derivative capable of giving origin to membrane bone tissue in this particular region of the shoulder-girdle. The only possible alternative explanation for the growing medial rims of the clavicles is to be considered in the light of the "Fasernknochen" of Weidenreich (1923). This explanation implies that the clavicles of larval and small postmetamorphic specimens, in which no clavicular progressive growth has yet taken place, are of cuticular origin alone, but that in adult specimens, in which the clavicles show active growth, these bones have a double origin. For the greater part they are pure cuticular derivatives to which "Fasernknochen" nodules (Fig. 5, cln) originating from the ventral aponeurosis by direct ossification, are added during later life. These nodules should then be regarded as ossifications of the ligamentous ventral aponeurotic tissue, and are then identical with what were formerly known as "sesamoid bones", such as the postpelvic Nobelian bones of *Ascapheus*, which De Villiers (1926) regards as "Fasernknochen". This hypothesis, however, does not satisfactorily explain the presence of the tuberosities, which certainly are ossifications of the clavicle sheath. It seems more logical to conclude that both the tuberosities and the growing medial rims of the clavicles are also cuticular derivatives, and that these additional structures originate from formative cuticular cells arising from the periosteum of the clavicles.

Nothing has yet been said about the origin of the limb and girdle musculature. In stages A and B the ventro-lateral parts of the myotomes, situated dorsal to the limb-bud region, seem to show proliferation of cells since the muscle bundles are much smaller and more numerous than in other parts of the myotomes (Fig. 10). The perimysial connective tissue binding the bundles to one another is also more densely dispersed in these particular regions of the myotomes. Do these phenomena represent proliferation of cells from the myotomes, later to form the girdle and limb musculature as described by Braus (1904) and Goodrich (1930)? It is histologically quite impossible

to distinguish myogenic cells of the limb-bud core from those of apparently myotomic origin. In any case, the girdle and limb musculature first appear as indistinct, thickened patches in the blastematous tissue of the limb-bud core.

THE DEVELOPMENT OF THE STERNUM

The adult anatomy and the ontogenesis of the sternum have frequently been investigated, and the results have varied somewhat. Many of the investigations on the sternum were carried out mainly in order to test Ruge's theory (1880), that the sternum is of costal origin. Even for *Amphibia*, in which ribs are feebly developed or entirely absent, a costal origin for the sternum has been claimed by some workers (Fuchs, 1926 b; Engler, op. cit.). Ruge's theory for the sternum of *Amphibia* was proved untenable by a large number of workers (see historical introduction). The sternum of *Xenopus* is certainly not of costal origin. De Villiers (1922, 1924) claimed that the ventral sternal elements of *Xenopus* are of zonal origin, and that they correspond to the same elements of the *Discoglossidae*, as exemplified by *Bombina(tor) pachypus* and *Alytes*. But quite rightly, he did not venture to generalize about the constant zonal origin of these elements in the *Anura*. In order to test the matter, the development of the sternum of *Bufo angusticeps*, as a representative of a non-discoglossid arciferan, was also investigated in the present research although the development of such a sternum has already been studied in *Bufo bufo asiaticus* by Hsiao (op. cit.).

As stated in the previous chapter, the sternum of *Xenopus* arises very late in ontogeny, when the rest of the shoulder-girdle has attained an advanced degree of development. The dorsal sternal elements seem to develop in direct continuity with the ventral ones. Numerous stages were investigated in the hope of finding the dorsal elements actually developing independently of the ventral ones, but with no success. The sternum arises as two sternal anlagen only, which later fuse to form the unpaired structure of the adult. In the past none of the workers on the ontogenesis of the sternum probably suspected that the ventral aponeurosis may be of great importance for the development of the sternum. In his work of 1922, for example, De Villiers repeatedly figured the ventral aponeurosis, without describing or realising the importance of this connective tissue entity as a formative sternal mother tissue.

Stage A: The two processûs epicoracoidei are vertically disposed in the lateral parts of the body wall and are therefore widely separated from each other mid-ventrally. The right and left anlagen of the ventral aponeurosis have not yet fused, while the linea alba is a broad, thin stretch of connective tissue, binding the ventral margins of the m. recti abdominis. The earliest anlagen of the sternum appear as two small patches of blastematous tissue, situated laterally to the postero-ventral margins of the processûs epicoracoidei (Fig. 18, vsa). These blastematous patches are embedded in a thickened part of the ventral aponeurosis (va), and are also in direct continuity with the perichondrium of the processûs epicoracoidei. In spite of the latter condition, the blastematous patches described above are to be regarded as originating from the ventral aponeurotic tissue. Even at this stage the hypaxonic

pectoral muscles are attached to the sternal anlagen as well as to the tissue of the ventral aponeurosis. It is quite probable that these earliest anlagen of the sternum correspond to the ventral or presternal elements (Blättchen) of the discoglossid sternum described by De Villiers (1922) in *Bombina (tor) pachypus* and in *Alytes*, and by Hsiao (op. cit.) in *Bombina orientalis*.

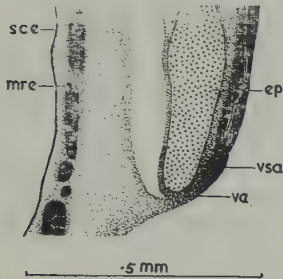


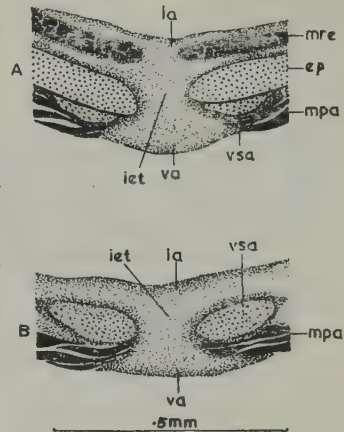
FIG. 18

Transverse section through the epicoraco-sternal region (stage A) to show the earliest anlage of the sternum. Abbreviations as for the previous figures.

Stage B: The two processûs epicoracoidei are considerably nearer to each other, with the result that their ventral ends now occupy a more horizontal position (Fig. 19, ep). The right and left anlagen of the ventral aponeurosis have fused mid-ventrally, forming a continuous stretch of tissue, situated between the medial margins of the hypaxonic appendicular and zonal muscles and of the processûs epicoracoidei (Fig. 19, va). The linea alba (la) is

FIG. 19

Transverse sections through the epicoraco-sternal region (stage B). A through the anterior procartilaginous parts of the ventral sternal elements. B through the posterior parts of the ventral sternal elements. Abbreviations as for previous figures.



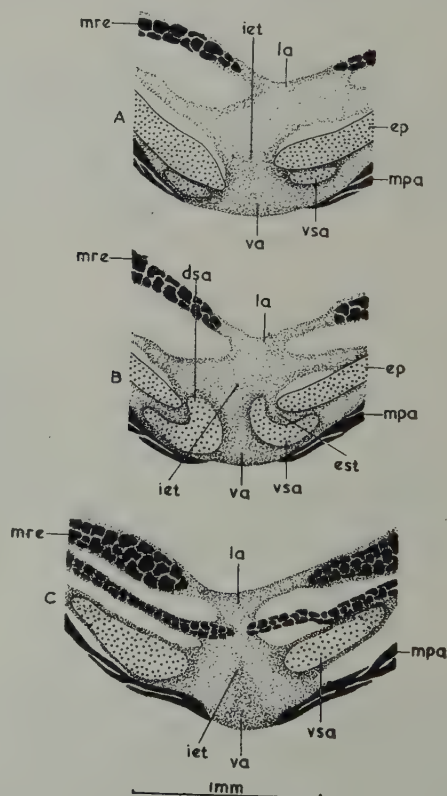
likewise thickened and somewhat vascularised; it contains a few large lymph spaces and a few small blood-vessels, and is broadly connected with the ventral aponeurosis by means of the interepicoracoidal tissue (iet). In the posterior interepicoracoidal region, therefore, there is a concentration of connective tissue originating from the ventral aponeurosis and from the linea alba, and it undoubtedly forms the mother tissue of the dorsal parts of the sternum. The sternal anlagen described in the previous stage are now procartilaginous, situated ventrally to the postero-medial ends of the processûs epicoracoidei; they are still embedded in the tissue of the ventral aponeurosis (Fig. 19A, vsa). These anlagen are produced backwards, posterior

to the hind margins of the processûs epicoracoidei, as two distinct and separate patches of procartilaginous tissue (Fig. 19 B, vsa). Sternal structures, comparable with the discoglossid dorsal sternal elements ("Hörner" of De Villiers, 1922) are therefore not yet present at this stage.

Stage C: This stage is essentially the same as the previous one, as regards the structure and extent of the linea alba, the ventral aponeurosis and the interepicoracoidal tissue (compare figures 19 and 20). Anterior to the sternal region the processûs epicoracoidei now overlap, but they remain separated from each other in the sternal region by the interepicoracoidal tissue. As in the previous stage, the ventral sternal elements (Fig. 20 A, vsa) first appear in section as two procartilaginous patches, situated ventrally to the medial margins of the processûs epicoracoidei (ep). If the sections are followed backwards, these procartilaginous structures are seen to chondrify (Fig. 20 B and C); they expand in a mediad direction and slightly embrace

FIG. 20

Transverse sections through the epicoraco-sternal region to show the development of the dorsal sternal elements and the formation of the sternal pouches (stage C). Abbreviations as for previous figures.



the postero-medial tips of the processûs epicoracoidei. Posterior to the latter the sternal anlagen are in the form of two cartilaginous patches embedded in the ventral aponeurosis and in the interepicoracoidal tissue (Fig. 20 C, vsa). It is remarkable that the right sternal anlage is larger than the left (see fig. 20 B and C).

The question immediately arises whether the medial expansion of the ventral elements (Fig. 20 B, *dsa*) are the homologues of the dorsal sternal elements ("Hörner") of the *Discoglossidae*. Since these medial expansions later develop in a dorso-lateral direction to form the roofs of the sternal pouches (see next stage), one is inclined to favour this homologisation, although the "Hörner" develop separately from the ventral sternal elements. In any case, the dorsal elements in *Xenopus* arise as the result of the progressive chondrification of the ventral elements in a mediad direction, for formative tissue of the ventral aponeurosis and of the interepicoracoidal tissue is changed to cartilage in the process.

Stage D: The ventral sternal elements have increased in size, while their medial expansions described in the previous stage have likewise become

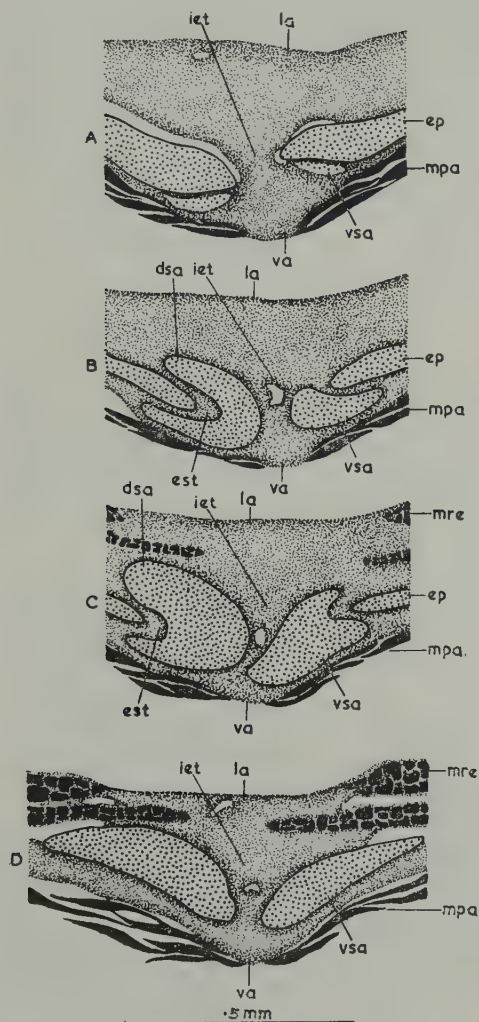


FIG. 21

Transverse sections through the epicoraco-sternal region to show the asymmetrical development of the sternal pouches, and the relations of the ventral aponeurosis, the linea alba and the interepicoracoidal tissues to one another (stage D). Abbreviations as for previous figures.

larger and embrace the medial tips of the processûs epicoracoidei completely, thus forming the roofs of the sternal pouches (Fig. 21 B and C). These latter, therefore, arise as the result of the progressive expansion of the ventral elements, first in a mediad and then in a dorso-lateral direction. As stated in the description of the previous stage, these medial and dorso-lateral expansions of the ventral elements (Fig. 21 B, C, *dsa*) are to be regarded as the homologues of the "Hörner" of the *Discoglossidae*, although they develop in continuity with the ventral elements: they are essentially chondrifications of the interepicoracoidal tissue (Fig. 21, *iet*). Posterior to the sternal pouch region the ventral sternal elements are produced backwards as two separate plate-like cartilages embedded in the ventral aponeurosis (Fig. 21 D, *vsa*). The right sternal pouch (Fig. 21 B, C, *est*) is better developed than the left.

Stage E: This stage of sternal development is found in completely metamorphosed individuals, in which the tail has been entirely resorbed. The right and left sternal anlagen have fused, forming the unpaired sternal apparatus characteristic of the adult condition (Fig. 8). The paired origin of the sternum is still evident, as its dorsal surface is grooved in a cranio-caudal direction (Fig. 8 C and D). Anteriorly complete sternal pouches are present for the reception of the posterior rims of the processûs epicoracoidei (Fig. 8 C, *est*). The hind part of the sternum, posterior to the processûs epicoracoidei, consists of a thin plate of cartilage lying between the *mm. recti abdominis* and the *portio abdominalis musculi pectoralis*. The ventral aponeurosis, the interepicoracoidal tissue and the *linea alba* are much less dense than in the previous stages (compare figures 8 and 21). The epicoraco-sternal mass (Fig. 8, *ecs*) binding the sternum to the processûs epicoracoidei represents unchondrified interepicoracoidal tissue. In all later stages the sternum is similar to its appearance in this stage, except that its lateral margins greatly increase in size, forming lateral sternal wings. Moreover, the roofs of the sternal pouches seem to disappear in late postmetamorphic and adult specimens (see fig. 7). The sternal pouches are thus reduced to sternal fossae (Fig. 7 C, *sf*); the reduction probably starts with the left pouch, as in a few specimens the roofs of the right pouches are rudimentary, while those on the left are entirely absent.

Although the available material of *Bufo angusticeps* was not old enough to enable one to investigate the sternal anatomy of young postmetamorphic and adult specimens, the development of the ventral and dorsal sternal elements could be traced. Judging from Hsiao's description (*op. cit.*) of the sternal development in *Bufo bufo asiaticus*, the sternum in this genus develops along approximately similar lines as that in the *Discoglossidae*, in which the sternum arises as two dorsal elements of myocommatous, and two ventral ones of zonal, origin (De Villiers, 1922). In *Bufo bufo asiaticus* (Hsiao, *op. cit.*) the first sternal elements to develop are the ventral ones, situated underneath the medial edges of the processûs epicoracoidei. Hsiao, however, states nothing about their origin. The dorsal elements develop in the myocommatous tissue of the *m. rectus abdominis*, their antero-median edges being united by means of a dense mass of connective tissue, situated interepicoracoidally. This tissue later chondrifies, with the result that anteriorly the sternal horns or dorsal sternal elements become synchondrotically fused with each other and with the ventral elements. The latter become reduced in size, apparently contribute very little to the formation of the adult sternum and later fuse

with the processûs epicoracoidei. The dorsal elements increase in size and form the adult sternal apparatus.

As may be expected, the sternal development of *Bufo angusticeps* agrees largely with that of *Bufo bufo asiaticus*. In the former species the earliest anlagen of the sternum are the ventral elements, situated ventrally to the postero-median edges of the processûs epicoracoidei (Fig. 22 A, vst).

FIG. 22

Transverse sections through the epicoraco-sternal region of *Bufo angusticeps* to show the earliest anlage of the sternum and the relations of the ventral aponeurosis, the linea alba and the inter-epicoracoidal tissues to one another. Abbreviations as for previous figures.

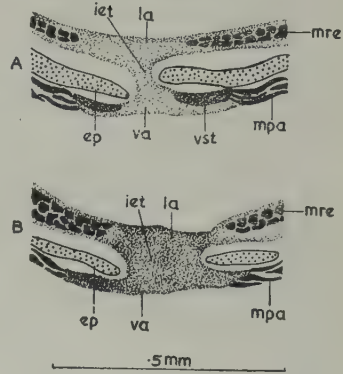
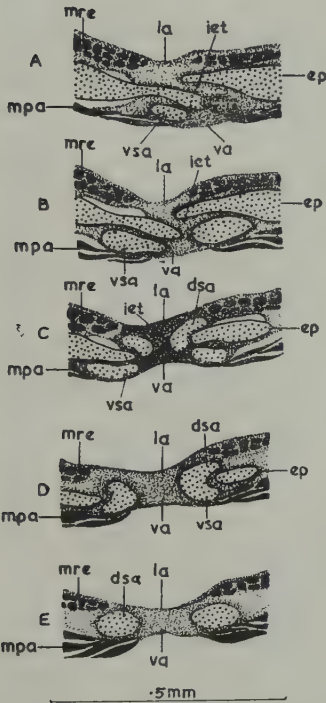


FIG. 23

Transverse sections through the epicoraco-sternal region of *Bufo angusticeps* to show the development of the dorsal and ventral sternal elements and the relations of the ventral aponeurosis, the linea alba and the interepicoracoidal tissues to one another. Abbreviations as for previous figures.

These elements, however, are not zonal in origin, as in the *Discoglossidae*, but are distinctly chondrifications of the ventral aponeurosis, separated from the processûs epicoracoidei by clear spaces, which resemble synovial cavities (see fig. 22). Unfortunately the subsequent reduction of these elements could not be followed. But that such a process is actually going on, is proved by the fact that the left element is already fused to the medial tip of the right processus epicoracoideus (Fig. 23, A). As in *Xenopus*, a concentration of

interepicoracoidally situated formative sternal tissue (Figures 21, 22, iet), originating from the linea alba and from the ventral aponeurosis, is formed in the posterior interepicoracoidal or sternal region. In the dorsal or linea alba niveau of this tissue the dorsal sternal elements chondrify (Fig. 23 C, dsa), and they may therefore be regarded as chondrifications of the linea alba. The chondrification then spreads into the rest of the interepicoracoidal tissue, so that the anterior tips of the horns are procartilaginously fused with each other and with the ventral elements (Fig. 21 C). The sternal horns are produced backwards as two cartilaginous bars (Fig. 23 E, dsa) lying partly in the linea alba and partly in the ventral aponeurosis, since these two connective tissue entities, otherwise separated, are fused posterior to the epicoracoidal region (see fig. 23 E).

From the above description of the sternal development of *Xenopus* and of *Bufo angusticeps*, it is evident that there is some similarity in the sternal development of the two genera and that of the *Discoglossidae*. The ventral sternal elements of the former correspond in topography, but not in origin, with the discoglossid ventral elements. In the former two genera these elements are chondrifications of the ventral aponeurosis, and are therefore not zonal derivatives, as in the *Discoglossidae*. It is therefore impossible to generalize about the ontogenesis of the ventral elements, as they apparently develop from "morphologically different" blastematos rudiments. In *Xenopus* the dorsal elements, developing in synchondrotic continuity with the ventral ones, arise as chondrifications of the interepicoracoidal tissue. In *Bufo angusticeps* they develop independently from the ventral elements and mainly as chondrifications of the linea alba. In the *Discoglossidae* they also develop separately as chondrifications in the myocommatous tissue of the m. rectus abdominis (De Villiers, 1922). The dorsal elements of *Xenopus* and *Bufo angusticeps* are therefore not the exact homologues of these structures in the *Discoglossidae*. The sterna of *Xenopus* and *Bufo angusticeps* are therefore autochthonous chondrifications of the ventral aponeurosis and of the interepicoracoidal tissue, and, in the latter genus, of the linea alba as well. If the discoglossid sternal development is regarded as primitive, that of *Xenopus* and of *Bufo angusticeps* must be regarded as caenogenetic, in terms of the Von Baer-Haeckel formulation of the fundamental law of biogenesis. The ontogenesis of the liopelmid sternum, which unfortunately is not known, should be of the greatest importance, since the most primitive sternal development will probably be found in this family. De Vos (1938, No. 2) stated that in the adult *Liopelma* the sternal styles are fused with the third pair of inscriptional ribs. This is reminiscent of the condition obtaining in lizards, as described by Van Gelderen (1925). This author maintains that the posterior part of the lacertid sternum (xiphisternum) is of costal origin since it develops in direct continuity with the ventral parts of the posterior ribs. Is that part of the liopelmid sternum fused to the ventral abdominal ribs, costal in origin and is this the most primitive condition in the *Anura*? It seems more logical to suspect that the sternum in the *Anura* (and in *Liopelma*) is never of costal origin, and that the liopelmid condition, in which the sternal styles are fused to the inscriptional ribs "need not be construed as evidence of a costal origin of that part of the anuran sternum . . ., but merely proves that any portion of the endoskeletal strata is essentially skeletogenous" (De Vos, 1938, No. 2). In the light of the above description of the sternal

development in *Xenopus* and *Bufo*, the costal origin of the sternum in these two genera at least is quite out of the question.

According to De Villiers (1922) the ventral elements become somewhat reduced in *Bombina(tor) pachypus* and in *Alytes*, and the adult sternal apparatus is represented mainly by the dorsal elements. In *Bufo bufo asiaticus* these elements are so far reduced that they are represented by two small nodules of cartilage fused with the processûs epicoracoidei, while the dorsal elements constitute the adult sternal apparatus (Hsiao, op. cit.). In *Xenopus* the dorsal elements tend to become reduced, and are entirely absent in the adult condition, while the ventral elements form the adult sternal apparatus.

In Noble's most recent classification of the *Salientia* (1931), *Xenopus* is classified under *Pipidae*. It is now generally accepted that the latter are neotenic, although they display various primitive features, such as opisthocoelous vertebrae (Noble, 1931), absence of an episternum (De Villiers, 1924), large size of the procoracoidal cartilages and the clavicalae, various characters of the skull (Kotthaus, op. cit.), of the musculature (Noble, 1922, Grobbelaar, 1924) and of the vascular system (Millard 1949). Neotenic features have been stressed by Escher (op. cit.) Noble (1922, 1931) and recently by Millard (1949). One of the most important neotenic features is the maintenance of an aquatic habitat throughout life (Millard, 1949). This is probably responsible for a large number of specializations or orthogeneses, which are to be regarded as adaptations to the aquatic life. A list of these adaptations was given by Millard (1949). One such orthogenesis listed by Millard, is the enormous development of the muscles for swimming. The front legs, on the contrary, are poorly developed, being used for feeding rather than for locomotion (Millard, 1949). It is probably this characteristic, a direct result of the neotenic aquatic habit of life, that is responsible for the tendency towards firmisterny, and the corresponding total or potential loss of the dorsal sternal elements in the *Aglossa*. This assumption then implies that firmisterny has been acquired more than once and for various reasons. The firmisternal *Polypedatidae*, for example, are arboreal (Noble, 1931). The *Firmisternia* are therefore not a natural group, and the mutual relations of the ventral halves of the shoulder-girdle cannot be used as a basis of classification, as already stressed by Noble as far back as 1922.

SUMMARY AND CONCLUSIONS

- 1 The shoulder-girdle of *Xenopus* is arcifero-firmisternal, as already stated by De Villiers (1922). The procoracoidal cartilages are articulated on the firmisternal, and the processûs epicoracoidei on the arciferous principle. A progressive tendency towards firmisterny is present in the *Aglossa* and has probably been acquired independently in the different genera (De Villiers, 1929).
- 2 The separating connective tissue between the cleithrum and the suprascapula disappears in some of the large, adult specimens investigated. The cleithrum then invades the suprascapula, resulting in the ossification of the latter. A distinct hinge, consisting of cartilaginous tissue, is present between the ventral margin of the suprascapula and the dorsal margin of the scapula.

- 3 The scapula is small, intensely ossified and fused with the lateral end of the clavícula, thus forming a secondarily undivided bone framing the glenoid cavity. The entity thus formed is not to be homologised with the primitive coracoscapula present in the *Liopelmidae* (Romer, 1931, De Vos, op. cit.) and in some *Embolomeri* (Romer, 1931), since it is not formed by the progressive downgrowth of the scapula into the pars coracoidea of the coracoidal plate.
- 4 In all the specimens investigated the scapula is pierced by a glenoid foramen, probably serving to regulate the pressure in the glenoid cavity during movement of the caput humeri within the latter. It is situated primarily between the ventral margin of the scapula and the cartilago paraglenoidalis; the intrascapular position is secondarily acquired as the result of the progressive downgrowth of the scapula into the cartilago paraglenoidalis. In the adult condition the latter is a small piece of cartilage, framing part of the glenoid cavity and separating the ventral end of the scapula from the dorsal end of the coracoid.
- 5 The smallness of the scapula is probably correlated with the aquatic habit, the latter being a neotenic feature. The smallness of the scapula is therefore probably the result of neoteny affecting a single structure.
- 6 The cleithrum was found to be very large and to be a derivative of the cutis. It is characteristically V-shaped, and actually meets the scapula, a small synovial cavity being present in the region of the scapulo-cleithral contact. The largeness of the cleithrum is very difficult to interpret. It may be a primitive feature, as the bone in question is very large in *Labyrinthodontia*. It may, however, be an adaptation to aquatic life, serving to strengthen the scapulo-suprascapular region of the shoulder-girdle, the scapula being very small. It serves as a point of attachment for a large number of muscles.
- 7 The clavícula is very large and invests the procoracoidal cartilage ventrally. Ontogenetically it was found to be a derivative of the cutis, developing in an islet of cuticular tissue secondarily separated from the main cutis in response to the development of the hypaxonic appendicular muscles. Even in completely adult specimens it shows progressive growth, as its dorsal surface is beset with large tuberosities, and its medial rim tends to grow into the ventral aponeurosis. The formative cuticular tissue responsible for the clavicular growth, is to be derived from the clavicular periosteum, the only unossified cuticular derivative capable of giving origin to membrane bone in that particular region of the shoulder-girdle. The largeness and mainly ventral position of the clavícula with respect to the procoracoidal cartilage is probably a primitive feature as already stated by De Villiers (1924, 1929), since the same condition obtains in *Labyrinthodontia* and in the primitive *Liopelmidae* (Romer, 1931, De Vos, op. cit.).
- 8 The procoracoidal cartilages are very large, and arise ontogenetically as independent chondrifications in the blastematous pars coracoidea. In adult specimens they are fused anteriorly for quite a distance, this part of the shoulder-girdle then being firmisternal, functionally as well as anatomically.

- 9 The processûs epicoracoidei are movably articulated on the arciferous principle as already stated by De Villiers (1924, 1929). According to my own investigations they arise as forwardly directed processes of the coracoidal cartilages and close the fenestrae obturatoriae medially. They are not interrupted either in the adult condition or in any stage of development after they have become fused with the procoracoidal cartilages anteriorly.
- 10 The coracoids are long, slender bones, each containing a large central marrow-cavity and several smaller ones. Like the procoracoidal cartilages they arise as independent chondrifications in the coracoidal plates, and together with the shaft of the humerus, are the first elements of the shoulder-girdle to ossify. They form the latero-posterior boundaries of the fenestrae obturatoriae.
- 11 Judging from the study of embryological material, the fenestra obturatoria conforms to the conception of a secondary fenestra ("Reduktionsfenster" of Fuchs), and arises in the coracoidal plate as a foramen pro nervo supracoracoideo, which later enlarges through the reduction of the tissue of the pars coracoidea. It is covered in larval and young postmetamorphic individuals by a primary membrana obturatoria ("Reduktionsmembran" of Fuchs), originating from blastema of the pars coracoidea. It is entirely absent in later post-metamorphic and in adult specimens.
- 12 The tissue forming the earliest anlage of the limb-bud probably originates from the axial mesenchyme. The routes of growth are probably the myocommata between the myotomes, and probably also the space between the ventral margins of the myotomes and the somatic coelomic epithelium. The latter route is also followed by the limb-bud nerve, which originates as a result of the fusion of two nerves passing from two consecutive spinal ganglia.
- 13 The ventral aponeurosis is a derivative of the mesenchyme, and the tissues forming the linea alba and the myocommata of the myotomes and of the m. rectus abdominis probably have a similar origin. Both in *Xenopus* and in *Bufo angusticeps* the ventral aponeurosis forms the mother tissue of the ventral sternal elements.
- 14 The interprocoracoidal and interepicoracoidal tissues, as well as the procoracoidal capsular tissue are derivatives of the ventral aponeurosis and of the linea alba. All these connective tissue entities are potentially skeletogenous. The capsular and interprocoracoidal tissues may chondrify as isolated patches, and their chondrification is furthermore responsible for the fusion of the anterior tips of the procoracoidal cartilages. The interepicoracoidal tissue is the mother tissue of a part of the sternum.
- 15 The sternum is cartilaginous throughout life, and arises as paired autochthonous chondrifications of the ventral aponeurosis and of the interepicoracoidal tissue. The first sternal rudiments to chondrify are the ventral ones, originating as chondrifications of the ventral aponeurosis. The dorsal elements, constituting the roofs of the sternal pouches, develop in synchondrotic continuity with the ventral elements and tend to disappear in old postmetamorphic and adult specimens.

Sternal pouches are therefore confined to larval and young post-metamorphic individuals and are reduced to sternal fossae during later life.

- 16 The absence or partial absence of the dorsal sternal elements in the *Aglossa* is probably the result of neoteny, and is correlated with the progressive tendency towards firmisterny, a tendency which has been attained independently by the different aglossal genera.
- 17 The ventral sternal elements constitute the adult sternum in *Xenopus*, while in *Bufo* and the *Discoglossidae* mainly the dorsal elements give rise to the adult sternal apparatus, the ventral ones tending to become reduced.
- 18 The mode of the sternal development of *Xenopus* is to be regarded as caenogenetic, if that of the *Discoglossidae* is regarded as primitive. The sternogenesis of the *Liopelmidae* is unfortunately not known. Since *Liopelma* has inscriptional ribs, and since its sternum is partially fused with these ribs (De Vos, op. cit.) it would be interesting to know whether its sternum is at least partially of costal origin, as is claimed by Van Gelderen for lizards.
- 19 It is impossible to generalize about the constant zonal origin of the ventral sternal elements, but these structures are autochthonous chondrifications of the ventral aponeurosis in *Xenopus* and in *Bufo angusticeps*. The importance of the ventral aponeurosis and of the interepicoracoidal tissue as formative sternal tissues has been overlooked by investigators on the origin of the sternum.
- 20 The epicoraco-sternal tissue is a derivative of the interepicoracoidal tissue.
- 21 The dorsal and ventral sternal elements, and consequently the sternal pouch of the right side, are larger than those of the left side, a condition that can probably be explained on mechanical grounds. As the right processus epicoracoideus generally overlaps the left one, the right sternal pouch will be better developed in order to prevent too much mutual displacement of the processus epicoracoidei.
- 22 The episternum is entirely absent in the *Aglossa*. De Villiers (1924) maintains that this condition is a primitive feature of the *Aglossa*.

It cannot be pretended that a study of the ontogenesis and adult anatomy of the breast-shoulder apparatus of a single genus can be conclusive of the conditions obtaining in the *Pipidae* as a whole. Since this family is admittedly neotenic, detailed comparison with the primitive *Anura*, such as the *Liopelmidae* and the *Discoglossidae* is dangerous, and the utmost care should be exercised not to homologise neotenic features of the latter two families. In spite of the neoteny of the *Pipidae*, however, comparison with the primitive anuran families can be very fruitful in elucidating morphological and ontogenetic problems in the *Pipidae*. Not only adult anatomical data, but also ontogenetic facts of all the pipid genera and of the *Liopelmidae* and *Discoglossidae* should be compiled to estimate the exact interrelationships of these three anuran families. It is regrettable that comparative anatomical and ontogenetic research on the *Liopelmidae* and on certain genera of the *Pipidae* has been somewhat

neglected, probably owing to the inaccessibility of material. Future investigations in this sphere of comparative anatomy should therefore be concentrated on the Liopelmidae and on the Pipidae.

ALPHABETICAL LIST OF ABBREVIATIONS

am	unchondrified part of axial mesenchyme
as	lateral wing of sternum
at	atrium
bl	bloodvessel
c	chondroblast
cb	cartilaginous bridge
ce	centrum
ch	caput humeri
cho	chorda dorsalis
cil	islet of cartilage
cj	cartilaginous hinge
cla	clavicula
cln	clavicular nodule embedded in ventral aponeurosis
cn	dorsal nerve cord
co	coracoid
coc	coracoidal cartilage
cp	cartilago paraglenoidalis
cs	corpus sterni
cu	cutis
cut	cell thickening in cutis
cvs	clavicle-sheath
dcl	dorsal flange of clavicle
dsa	dorsal sternal element
eca	ectoderm of atrium
ecs	epicoraco-sternal tissue
ect	ectoderm of limb-bud
ep	processus epicoracoideus
est	sternal pouch filled with epicoraco-sternal tissue
fo	fenestra obturatoria
fpro	fused parts of procoracoidal cartilages
fs	glenoid foramen
gc	glenoid cavity
iet	interepicoracoidal tissue
io	incisura obturatoria
ipt	interprocoracoidal tissue
la	linea alba

lb	limb-bud
m	matrix
mo	membrana obturatoria
mpa	portio abdominalis musculi pectoralis
mre	m. rectus abdominis
my	dorsal part of myocomma
myi	ventro-lateral part of myocomma
myo	myotome
myr	space between ventral border of myotome and somatopleuric coelomic epithelium
nh	nerves to front leg
npc	n. supracoracoideus
nps	nerve to pars scapularis
ns	brachial plexus
os	ossification in suprascapula
osf	ossification in procoracoidal cartilage
ost	osteoblast
pa	pars appendicularis
pc	pars coracoidea
pct	procoracoidal capsular tissue
pn	pronephros
pro	procoracoidal cartilage
ps	pars scapularis
psc	pars scapulo-coracoidea
sc	scapula
sca	synovial cavity in region of scapula-cleithral articulation
sce	somatopleuric coelomic epithelium
scp	suprascapula
sm	separating membrane
smi	
tb	thickened blastematous patch of tissue
tu	clavicular tuberosity
va	ventral aponeurosis
vcl	ventral flange of cleithrum
ve	dorsal part of vertebra
vsa	ventral sternal element.

LIST OF LITERATURE CITED

- Bogoljubski, S. 1914. Brustbein- und Schultergürtel-entwicklung bei einigen Lacertiliern. Z. wiss. Zool., 110 : 620.
- Boulenger, G. A. 1882. Catalogue of the Batrachia Salientia s. Caudata in the collection of the British Museum. London.

- Braus, H. 1904. Die Entwicklung der Form der Extremitäten und des Extremitätenskeletts. Hertwigs Handb. d. vergl. u. exp. Entw. der Wirb., Jena, 3 : 167.
- Braus, H. 1909. Gliedmaszenpfpung und Grundfragen der Skelettbildung. Morph. Jb., 39 : 155.
- Braus, H. 1919. Der Brustschulterapparat der Froschlurche. Sitzungsber. Heidelberg. Akad. Wiss., Abt. B, Abh., 15 : 1.
- Bremer, J. L., and Weatherford, H. L. 1944. A Textbook of Histology. Blakiston Company, Philadelphia.
- Broom, R. 1932. The Mammal-like Reptiles of South Africa and the Origin of Mammals. H. F. & G. Witherby, London.
- Cope, E. D. 1865. Sketch of the primary groups of Batrachia salientia. Nat. Hist. Rev., Vol. 4.
- De Villiers, C. G. S. 1922. Neue Beobachtungen über den Bau und die Entwicklung des Brustschulterapparates bei den Anuren, insbesondere bei Bombinator. Acta zool. Stockh., 3 : 153.
- De Villiers, C. G. S. 1924. On the Anatomy of the Breast-shoulder apparatus of Xenopus. An. Trans. Mus., 10 : 197.
- De Villiers, C. G. S. 1925. Nuwe navorsinge oor die bors-skouerapparaat van die Anura. S. Afr. J. Sci., 22 : 226.
- De Villiers, C. G. S. 1925. On the Development of the "Epipubis" of Xenopus. Ann. Trans. Mus., 11 : 61.
- De Villiers, C. G. S. 1926. Some Aspects of the Morphology and Ontogeny of the skeletogenous strata. S. Afr. J. Sci., 23 : 61.
- De Villiers, C. G. S. 1929. The Comparative Anatomy of the Breast-shoulder apparatus of the three Aglossal Anuran Genera: Xenopus, Pipa and Hymenochirus. Ann Trans. Mus., 13 : 37.
- De Villiers, C. G. S. 1934. On the Morphology of the Epipubis, the Nobelian Bones and Phallic Organ of Ascaphus truei Stejneger. Anat. Anz., 78 : 23.
- De Vos, C. M. 1938. The zonal and sternal skeleton of the Liopelmidae (Anura). Anat. Anz., 87 : 54.
- De Vos, C. M. 1938. The inscriptional ribs of Liopelma and their bearing upon the problem of abdominal ribs in Vertebrata. Anat. Anz., 87 : 82.
- Dreyer, T. F. 1914. The Morphology of the Tadpole of Xenopus laevis. Trans. roy. Soc. S. Afr., 4 : 241.
- Engler, E. 1929. Untersuchungen zur Anatomie und Entwicklungsgeschichte des Brustschulterapparates der Urodelen. Acta zool. Stockh., 10 : 143.
- Escher, K. 1925. Das Verhalten der Seitorgane der Wirbeltiere und ihrer Nerven beim Uebergang zum Landleben. Acta zool. Stockh., 6 : 307.
- Fuchs, H. 1912. Beiträge zur Entwicklungsgeschichte und vergleichenden Anatomie des Brustschulterapparates der Wirbeltiere. Erste Mitteilung: Ueber die Entwicklung der Clavicula bei Talpa europea und Erinaceus europaeus (nebst einigen vergleichend-anatomischen Bemerkungen). Z. Morph. Anthr. Sonderh., 2 : 141.
- Fuchs, H. 1922. Beiträge zur Entwicklungsgeschichte und vergleichenden Anatomie des Brustschulterapparates der Wirbeltiere. Zweite Mitteilung:

- Ueber den Schulter-gürtel der Amphibia anura, nach Untersuchungen am braunen Grasfrosche (*Rana fusca*): I Suprascapula und Cleithrum, Procoracoid und Thoracale ("clavicula"). Z. Morph. Anthr., 22 : 283.
- Fuchs, H. 1924. Beiträge zur Entwicklungsgeschichte und vergleichenden Anatomie des Brustschulterapparates der Wirbeltiere. Dritte Mitteilung: Ueber den Schulter-gürtel der Amphibia anura, nach Untersuchungen am braunen Grasfrosche (*Rana fusca*): II Cartilago procoracoidea und Os thoracale ("Clavicula"). Z. Morph. Anthr., 24 : 83.
- Fuchs, H. 1926. Beiträge zur Entwicklungsgeschichte und vergleichenden Anatomie des Brustschulterapparates der Wirbeltiere. Fünfte Mitteilung: Ueber den Schultergürtel der Amphibia anura: III. Von der natürlichen Unterbrechung der Cartilago procoracoidea und von dem Fenster am Schultergürtel der *Rana fusca*. Anat. Anz., 61 : I.
- Fuchs, H. 1926 b. Beiträge zur Entwicklungsgeschichte und vergleichenden Anatomie des Brustschultergürtels der Wirbeltiere. Sechste Mitteilung: Von der Entwicklung und vergleichend-anatomischen Bedeutung des Praezonales am Brust-schultergürtel der Amphibia anura (nach Untersuchungen am braunen Grasfrosche, *Rana fusca*). Verh. anat. Ges. Jena, Ergänzungsheft zum Anat. Anz., 61 : 119.
- Fuchs, H. 1927. Beiträge zur Entwicklungsgeschichte und vergleichenden Anatomie des Brustschultergürtels der Wirbeltiere. Siebente Mitteilung: Von der Fenstern im ventralen Abschnitte des Schultergürtels der Landwirbeltiere, insbesondere der Amphibien, Saurier und Testudinaten. Nebst Bemerkungen über die Begriffe „Homologie“ und „Blastem“. Anat. Anz., 64 : 305.
- Fürbringer, M. 1873. Zur vergleichenden Anatomie der Schultermuskeln. I. Theil. Jena. Z. Naturw., 7 : 273.
- Fürbringer, M. 1874. Zur vergleichenden Anatomie der Schultermuskeln. II. Theil. Jena. Z. Naturw., 8 : 175.
- Gladstone, R. J., and Wakeley, C. P. G. 1932. The Morphology of the sternum and its Relation to the Ribs. J. Anat. Lond., 64 : 508.
- Goodrich, E. S. 1930. Studies on the Structure and Development of Vertebrates. Macmillan and Co., London.
- Gaupp, E. 1896. A. Ecker's und R. Wiedersheim's Anatomie des Frosches. Erste Abt., Vieweg und Sohn, Braunschweig.
- Götte, A. 1875. Die Entwicklungsgeschichte der Unke. Leipzig.
- Grobbelaar, C. S. 1924. Beiträge zu einer anatomischen Monographie der „*Xenopus laevis*“ (Daud.). Z. ges. Anat. I. Abt., 72 : 131.
- Hamilton, W. J., Boyd, J. D., and Mossman, H. W. 1945. Human Embryology. Heffer & Sons, Cambridge.
- Hoffman, A. C. 1935. Oor die non-homologie van die medioventrale presonale skeletelemente by die Amfibië, Anura en Urodela. Soël. Nav. Nas. Mus. Bloemfontein, 1 : 3.
- Hoffman, A. C. 1936. Die anatomie van die skouergordel en die ontwikkeling van die sternum by die Urodela — *Cryptobranchus alleganiensis* en *Necturus maculatus*. Soël. Nav. Nas. Mus. Bloemfontein, 1 : 33.

- Howell, A. B. 1935. Morphogenesis of the shoulder Architecture. Part III. Amphibia. Quart. Rev. Biol., 10 : 397.
- Hsiao, S. D. 1933-1934. A comparative study of the Pectoral Region of some typical Chinese Salientia. Peking nat. Hist. Bull., 8 : 169.
- Jarvik, E. 1944. On the Exoskeletal shoulder-girdle of Teleostomian Fishes, with special Reference to Eusthenopteron Foordi Witheaves. K. svenska Vetenskapsakad. Handl., Tredje Serien, Bd. 21. No. 7, p. 3.
- Juhn, M. 1923. Die Entwicklung des Sternums bei Lacerta. Acta zool. Stockh., 4 : 65.
- Kälin, J. A. 1929. Ueber den Brustschulterapparat der Krokodile. Acta zool. Stockh., 10 : 343.
- Knopfli, W. 1918. Entwicklung des Brustschulterskelettes bei den Vögeln. Jena. Z. Naturwiss., 55 : 577.
- Kotthaus, A. 1933. Entwicklung des Primordial-craniums von *Xenopus laevis* bis zur Metamorphose. Z. wiss. Zool., Abt. A, 144 : 510.
- Lignitz, W. 1897. Die Entwicklung des Schultergürtels beim Frosch. Inaugural-dissertation. Leipzig.
- Maximow, A. A., and Bloom, W. 1930. A Textbook of Histology. W. B. Saunders Company, Philadelphia.
- Millard, N. 1941. The Vascular Anatomy of *Xenopus laevis* (Daudin.). Trans. roy, Soc. S. Afr., 28 : 387.
- Millard, N. 1949. The Development of the Venous System of *Xenopus laevis*. Trans. roy, Soc. S. Afr., 32 : 55.
- Nauck, E. Th. 1928. Beiträge zur Kenntnis des Skeletts der paarigen Gliedmaszen der Wirbeltiere. Morph. Jb., 60 : 61.
- Noble, G. K. 1922. The phylogeny of the Salientia: I. The osteology and the thigh musculature; their bearing on classification and phylogeny. Bull. Amer. Mus. nat. Hist., 46 : 3.
- Noble, G. K. 1925. The evolution and dispersal of the frogs. Amer. Nat., 59 : 265.
- Noble, G. K. 1926. The pectoral girdle of the Brachycephalid frogs. Amer. Mus. Novit., No. 230, p. 1.
- Noble, G. K. 1931. The Biology of the Amphibia. McGraw-Hill Book Company, New York and London.
- Parker, W. K. 1868. A monograph of the structure and development of the shoulder-girdle and sternum in the Vertebrata. Ray Society, London.
- Paterson, N. F. 1939. The head of *Xenopus laevis*. Quart. J. micr. Sci., 81 : 162.
- Proctor, J. B. 1921. On the variation of the scapula in the Batrachian groups Aglossa and Arcifera. Proc. zool. Soc. Lond., p. 197.
- Roggenbau, C. 1926. Zur Frage nach einem Episternalapparat nebst einer Bemerkung über die Cartilagines epicoracoideae am Brustschultergürtel der anuren Amphibien nach Beobachtungen am braunen Grasfrosch (*Rana fusca*). Anat. Anz., 61 : 84.
- Roggenbau, C. 1926. Einige Beobachtungen über die Verbindungen der Cartilago praezonalis mit den Procoracoidspangen und des Sternums mit den

- Coracoidplatten am Brustschulterapparat des braunen Grasfrosches (*Rana fusca*). Z. mikr. — anat. Forsch., 6 : 409.
- Romer, A. S. 1924. Pectoral limb musculature and shoulder-girdle structure in Fish and Tetrapods. Anat. Rec., 27 : 119.
- Romer, A. S. 1933. Vertebrate Paleontology. University of Chicago Press, Chicago.
- Rotmann, E. 1931. Die Rolle des Ektoderms und Mesoderms bei der Formbildung der Kiemen und Extremitäten von Triton. Z. wiss. Biol., 124 : 747.
- Ruge, E. 1902. Die Entwicklungsgeschichte des Skeletes der vorderen Extremität von *Spinax niger*. Morph. Jb., 30 : 1.
- Schmalhausen, J. 1917. On the dermal bones of the shoulder girdle of the Amphibia. Institute of Comparative Anatomy, University of Moscow.
- Stannius, H. 1856. Handbuch der Anatomie der Wirbeltiere, Zweites Buch: Zootomie der Amphibien. In Siebold und Stannius: Handbuch der Zootomie, Berlin.
- Van der Horst, C. J. 1934. The lateral-line nerves of *Xenopus*. Psychiat. neurol. Bl., Amst., Nos. 3 & 4, p. 3.
- Van Gelderen, Chr. 1923. Over de ontwikkeling van het sternum by reptiliën. Koninkl. Akad. Wetensch. Amst. — Natuurk. Afd., 30 : 113.
- Van Gelderen, Chr. 1925. Die Entwicklung des Brustschulterapparats bei Sauriern. Anat. Anz., 59 : 495.
- Weidenreich, F. 1923. Ueber den Begriff „Knochen“ und die Beziehungen des Knochengewebes zu Bindegewebe und Knorpel. Verh. anat. Ges. Jena, Ergänzungsheft zum Anat. Anz., 57 : 138.
- Wiedersheim, R. 1892. Das Gliedmaszenskelett der Wirbeltiere mit besonderer Berücksichtigung des Schulter- und Beckengürtels bei Fischen, Amphibien und Reptilien. Fischer, Jena.

